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Tool Use in Non-Human Primates (*Pan Troglodytes*) as a Model for Studying Cultural Evolution

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Antes de que habláramos, nuestras manos ya decían.
Golpeaban, transformaban y enseñaban.
Hoy las vemos aún: en chimpancés que aprenden unos de otros,
en lascas que cortan el silencio de la tierra.
Cultura sin palabras. Patrimonio sin símbolos.
La memoria, empieza en los dedos.

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Abstract

Tool use in non-human primates constitutes a key field for understanding the origins of material culture and the dynamics of social transmission. Over the past decades, numerous studies have documented diverse technical repertoires in species such as capuchins, orangutans, and macaques, but it is in chimpanzees (*Pan troglodytes*) that this diversity reaches a level of complexity particularly relevant to cognitive archaeology. Nevertheless, many questions remain about which individual and social factors shape the emergence and diffusion of these behaviours. This dissertation addresses this issue through an experimental study conducted at Fundació Mona (Riudellots de la Selva, Girona), a rescue and rehabilitation centre for chimpanzees. Two stable social groups, comprising a total of ten individuals, were presented with a novel instrumental task requiring the sequential use of two different tools to obtain a food reward. Both technical variables (selection, transport, modification, and use of tools) and social variables (presence of observers or transfers) were recorded in order to evaluate the relationship between social context and technical performance. Here we show that participation and technical success were not evenly distributed within the groups, but rather concentrated in specific individuals, often characterised by greater prior experience or social tolerance. We also found a preference for flexible tools and patterns of tool transfer among conspecifics. Predictive analyses further indicated that variables such as age, sex, number of observers, and repeated exposure significantly influenced both the likelihood of success, and the strategies adopted. These findings reinforce the view that tool use in chimpanzees depends on a complex interaction between individual and social factors, and that controlled captivity can provide valuable insights into the conditions that precede cultural transmission. Overall, the study contributes a comparative framework for behavioural archaeology and suggests that the antecedents of human material culture lie in gradual processes already present in other primates.

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1. INTRODUCTION AND OBJECTIVES

The study of early lithic technologies constitutes a key avenue of research for tracing the origins of human cognition and material culture. While the manufacture and use of stone tools were long assumed to be exclusive traits of the genus *Homo*, a growing body of archaeological evidence suggests that the roots of technological behaviour extend much further back in time (Lewis & Harmand, 2016). One of the earliest indications comes from the Dikika site, where cut marks and percussion traces on faunal remains dated to 3.4 million years ago, and attributed to *Australopithecus afarensis*, point to an incipient use of tools for carcass processing (McPherron et al., 2010). Shortly thereafter, the Lomekwian industry at Lomekwi 3 (Kenya, 3.3 Ma) revealed an unexpectedly early diversification of lithic production, expanding our understanding of pre-Oldowan technological capacities (Harmand et al., 2015). This discovery has been further contextualised by recent reviews emphasising percussive behaviours as a widespread foundation for early lithic technology, linking primate pounding to the emergence of the first archaeological industries (Harmand & Arroyo, 2023).

The earliest known *Homo* mandible, discovered at Ledi-Geraru (Ethiopia) and dated to 2.8 Ma, further situates hominin evolution in a regional context where Oldowan artefacts dated to 2.6 Ma had already been documented at nearby Gona (Semaw et al., 1997; 2003). These findings have been strengthened by more recent discoveries of both *Australopithecus* and *Homo* in the same area (Villmoare et al., 2025), underscoring the deep entanglement between hominin biological and technological evolution. Beyond East Africa, discoveries from Nyayanga (Kenya) confirm the presence of Oldowan tools associated with *Paranthropus* and diverse subsistence strategies, thereby extending the ecological and behavioural breadth of early stone tool use (Plummer et al., 2023). Even more notably, lithic assemblages from Sulawesi (Indonesia), dated between 1.04 and 1.48 Ma, point to an early technological dispersal beyond Africa (Hakim et al., 2025).

Taken together, these findings suggest that the development of lithic technology was not a linear trajectory confined to *Homo*, but rather a mosaic process involving multiple hominin taxa and contexts. A recent analysis highlights that stone tool complexity remained relatively low until around 600,000 years ago, when it began to increase markedly; this threshold has been interpreted as evidence that the human lineage had

entered a phase of reliance on cumulative culture during the Middle Pleistocene (Paige & Perreault, 2024). Such evidence broadens our perspective on the emergence of technical behaviours, situating them within a deeper evolutionary continuum that links human technological traditions to the capacities of other primates. This comparative framework is therefore essential for reinterpreting the origins of material culture.

Over the past decades, comparative primate research has undergone a sustained expansion, fuelled by the integration of systematic field observations with controlled experimental approaches in captivity. The meticulous documentation of technical behaviours and their modes of social transmission in chimpanzees (*Pan troglodytes*), orangutans (*Pongo spp*.), gorillas (*Gorilla spp*.), and capuchin monkeys (*Sapajus* and *Cebus*) has challenged the presumed exclusivity of humans in domains such as instrumental learning, technical innovation, and the emergence of group-specific cultural traditions (Boesch & Tomasello, 1998; Whiten et al., 1999; van Schaik et al., 2003). More recent contributions have not only extended the behavioural repertoire under scrutiny but also underscored the intricate interplay of social, ecological, and individual variables underlying the acquisition and maintenance of such practices (Hobaiter et al., 2014; Koops et al., 2022; Lamon et al., 2017). Taken together, this corpus of research compels us to conceptualise culture as an evolutionary phenomenon transcending humanity, with origins that predate our genus.

Chimpanzees (*Pan troglodytes*) provide a key model for exploring the foundations of material culture and tool use. Their close genetic relationship to humans (Prüfer et al., 2012), together with marked behavioural flexibility and strong capacities for observation and skill transmission, makes them particularly well suited to investigating how technical practices emerge, spread, and stabilize within social groups. Evidence further shows that chimpanzees sustain diverse and stable cultural repertoires while also adapting them to ecological and social change, pointing to a greater cultural plasticity than previously assumed (Lamon et al., 2017; Luncz & Boesch, 2014). From this perspective, cultural evolution can be understood not as a sharp discontinuity but as a gradual and shared process across primates, with human culture representing a quantitatively more complex expression within a broader evolutionary continuum (Whiten, 2017a).

The concept of culture has been studied from diverse and multidisciplinary perspectives, and it has generated considerable debate when applied to non-human species. Traditionally, anthropology has defined culture as a set of knowledge, practices, values, and symbols transmitted socially within a human group, often through language and formal institutions (Kroeber & Kluckhohn, 1952; Tomasello, 1999). By contrast, comparative research has adopted a more operational and behavioural definition: culture is understood as patterns of behaviour that vary across groups and can only be explained through social transmission, excluding ecological or genetic influences (Whiten et al., 1999; Laland & Janik, 2006). This functional approach has been essential in recent studies, which have established theoretical frameworks in which primate culture is assessed through the method of exclusion and the identification of behavioural variation not attributable to alternative factors (Koops et al., 2022; Whiten, 2021). Accordingly, culture is conceptualized as a continuous evolutionary process rather than an exclusively human property, allowing us to identify simplified forms of cultural transmission in non-human species such as chimpanzees, macaques, or gorillas (Boesch, 2012).

Social learning, defined as the modification of an individual's behaviour through observation or interaction with others (Heyes, 1994), has been central to understanding the transmission of cultural behaviours. Traditionally, mechanisms such as imitation and emulation (Tomasello, 1999; Hoppitt & Laland, 2013) have been used to classify learning processes in primates. However, recent research has demonstrated that social tolerance and exposure to diverse models are crucial in facilitating the acquisition of complex technical behaviours: young chimpanzees learn more effectively when they are able to observe tolerant and varied models (Nodé-Langlois et al., 2025). Moreover, in experimental settings, some chimpanzees have succeeded in solving sequential tasks that they had been unable to innovate individually, further underscoring the indispensable role of social models (van Leeuwen et al., 2024). These contributions go beyond simplified views of social learning and instead highlight the importance of social context and model characteristics in shaping the dynamics of non-human cultural transmission. This perspective provides a conceptual bridge towards understanding cumulative culture, by showing that the mechanisms enabling cultural stability also set the stage for its progressive elaboration.

Building on this perspective, one of the central debates in cultural evolution concerns the distinction between cumulative and non-cumulative culture. The former, often regarded as a hallmark of humans, is defined by the ability to transmit information and techniques with sufficient fidelity to allow their progressive improvement across generations, a process commonly referred to as the "ratchet effect" (Tomasello et al., 1993a; Tennie et al., 2009). In contrast, non-cumulative culture, documented in other primate species, is characterised by the presence of innovations that, although occasionally conserved, rarely undergo sustained refinement or combination. Recent studies have provided a more nuanced picture: experimental work has shown that chimpanzees can maintain technical improvements in relatively simple collective tasks, yet such improvements tend to plateau when problem complexity increases (Davis et al., 2016). Other studies have highlighted the role of ecological conditions and social tolerance as potential catalysts that enable a limited accumulation of technical knowledge (Dean et al., 2012; Vale et al., 2021). This ongoing debate is fundamental to understanding the limits and potential of cultural transmission in non-human primates and serves as a key interpretative framework for the present study.

The use of animal models in comparative research has been central to identifying cognitive and social traits shared with humans. Species such as chimpanzees, orangutans, and capuchins exhibit capacities to form complex social networks, solve problems, cooperate, and transmit technical knowledge (de Waal, 2001; Byrne & Whiten, 1988). In particular, studies on non-human primates allow for empirical investigation of which of these abilities might have been present in early hominins and how they could have formed the foundation for the emergence of material culture. Recent research has further advanced this perspective by examining, for example, the relationship between social structure and network dynamics (Canteloup et al., 2021), or the impact of behavioural plasticity on responses to novel ecological and technical challenges (Gruber et al., 2019). This approach provides a robust comparative framework that bridges primatology with palaeoanthropology and cognitive archaeology, thereby enabling the formulation of testable hypotheses on the origins and evolution of technical practices.

Several non-human primate species have demonstrated stable and socially transmitted forms of tool use, often differing across populations. Sumatran orangutans employ

modified branches to extract seeds, probe holes, or access insects, with behavioural variability depending on region and social group (van Schaik et al., 2003; Schuppli et al., 2016). South American capuchins (*Sapajus spp*.) use stones as pounding tools to crack nuts, as well as sticks to obtain honey or insects (Fragaszy et al., 2004; Ottoni & Izar, 2008). In an Asian context, Japanese macaques from Koshima have been documented using stones to crack open fruits and washing food items in water, behaviours transmitted socially and exhibiting intergroup variation (Kawai, 1965; Leca et al., 2007). Taken together, these cases demonstrate that material culture is not exclusive to chimpanzees but also manifests in several other primate species, with patterns of innovation, transmission, and maintenance that can be systematically compared. Nevertheless, it is in chimpanzees that such technical repertoires reach an unparalleled level of diversity and complexity.

Among all non-human primate species, chimpanzees (*Pan troglodytes*) stand out for the diversity, complexity, and social context of their technical repertoire. More than 40 distinct tool-use behaviours have been documented across populations, including termite fishing with twigs, nut-cracking with stone hammers, dental cleaning with plant stems, leaf-sponging for water extraction, and even sequential tool use, known as tool sets, to achieve specific goals (Boesch & Boesch, 1990; Sanz et al., 2004; Carvalho et al., 2009). These behaviours not only involve fine motor skills and knowledge of material properties, but also social processes of transmission, as many individuals acquire them through observing and interacting with more experienced conspecifics (Whiten et al., 1999; Hobaiter et al., 2014). Furthermore, the geographical variation in technical repertoires, documented in populations separated by hundreds of kilometres, reinforces the hypothesis of the existence of non-human cultures, with their own dynamics of maintenance and innovation (Whiten et al., 2001).

Within the chimpanzee's technical repertoire, behaviours involving the sequential use of more than one tool to achieve a specific goal, commonly referred to as tool sets or tool sequences, represent one of the most complex forms of tool use documented in non-human primates. These patterns require not only knowledge of the properties and functions of each tool, but also prior planning and precise motor coordination to execute the actions in a specific order (Boesch, 1991; Sanz et al., 2009). Documented examples include sequences that combine sticks to perforate and extract termites, leaf sponges to

collect liquids, or rigid and flexible tools to manipulate complex devices. The acquisition of such skills typically occurs through social learning processes, with a prominent role of observation and joint participation, and shows stable transmission within groups (Hobaiter et al., 2014; Biro et al., 2003). Although these behaviours do not reach the levels of technical accumulation characteristic of humans, they reinforce the idea that chimpanzees are able to integrate and coordinate multiple technical skills, thereby providing a relevant model for understanding the evolutionary precursors of lithic technology.

The accumulated evidence on tool use and social transmission in chimpanzees demonstrates a highly diverse technical repertoire, shaped by ecological variation and sustained through group-level learning processes (Boesch & Boesch, 1990; Whiten et al., 1999; Humle et al., 2009; Whiten, 2017b; Koops et al., 2023). Nevertheless, important questions remain regarding how these behaviours emerge, which individual and social factors modulate their diffusion, and to what extent such dynamics can be modelled and analysed in controlled contexts. Captive studies provide a unique opportunity to combine high experimental control with the preservation of naturalistic social interactions, allowing detailed evaluation of variables such as session number, tool type, or the presence of observers on both technical success and participation in the task (Whiten et al., 2005; Hopper et al., 2015a; Tennie et al., 2020).

To address these questions, a study was conducted at Fundació Mona (Riudellots de la Selva, Girona), a rescue and rehabilitation centre for chimpanzees that maintains stable social groups in conditions of controlled captivity, replicating natural social dynamics. Two mixed social groups, each composed of five individuals, participated in the study. The experimental task, designed as a novel form of enrichment, consisted of a complex instrumental challenge that required the sequential use of two different tools to obtain a food reward. In this study, not only the type of tool and its function were recorded, but also the duration of interaction, the modifications performed, the presence of observers, and the dynamics of transfer. This detailed record makes it possible to simultaneously analyse the technical and social dimensions, exploring the relationship between technical success, social context, and individual profiles.

Although conducted in a captive context, this study was designed to preserve conditions as naturalistic and spontaneous as possible. Unlike strictly laboratory-based experiments, individuals were not isolated or placed in unfamiliar settings; rather, the task was introduced within their established social groups as a form of enrichment. This approach seeks to balance experimental control with ecological validity, enabling a systematic assessment of tool use while maintaining ethologically relevant conditions. Such a design allows us to evaluate not only technical performance but also the spontaneous emergence of behaviours in a context that better approximates the dynamics of wild chimpanzee groups.

The principal aim of this study is to evaluate, in a spontaneous manner, chimpanzees' engagement with a novel task related to tool use, which requires the execution of a sequence of actions. On the one hand, the analysis focuses on success in extraction, exploration patterns, and technical behaviours such as tool transport and modification. On the other hand, it also examines whether social and demographic traits, such as age, sex, group membership, the number of observers or the transfer tools, could influence task resolution, incorporating predictive models for transport and modification in line with current trends in primate research on technical learning (Whiten, 2017a; Tennie et al., 2020).

Given the exploratory nature of this study and the limited number of previous studies on comparable tasks, we anticipated that (i) participation and technical success would be concentrated in a subset of individuals rather than evenly distributed across the group; (ii) individuals would preferentially employ flexible tools over rigid ones; (iii) if the structure of the task was understood, successful solutions would involve the use of the rigid tool first followed by the flexible one; and (iv) experience across sessions, as well as demographic and social variables, could modulate the likelihood of participation, the choice of tools, and the strategies employed.

This approach enables the documentation of both individual and group dynamics in task performance and provides relevant insights into processes of individual learning and the conditions that precede cultural transmission in non-human primates (Hopper et al., 2015b; Gunhold et al., 2014).

To address this research in a systematic manner, the dissertation is organized into several sections. The theoretical framework provides a critical review of previous studies on tool use in non-human primates, adopting a comparative perspective that includes capuchins, macaques, orangutans, gorillas, and, ultimately, chimpanzees. This overview situates the species under study within a broader spectrum of technical behaviours and cultural traditions documented across primate taxa. Subsequently, the concept of culture is examined from multiple disciplinary perspectives, anthropology, psychology, and biology, in order to establish an operational definition applicable to non-human species. A historical contextualization of primate research is also presented, alongside a discussion of the value of field studies compared to those conducted in captivity, as well as the methodologies employed to detect and analyse forms of social transmission.

The Materials and Methods section describes the experimental design, the chimpanzee groups under study, and the analytical tools applied, including systematic observation in a controlled environment, data recording procedures, and statistical modelling. The Results present the observed patterns of tool use and learning profiles, while the Discussion interprets these findings in light of the scientific literature and current debates on non-human culture, maintaining a comparative perspective that bridges primatology with palaeoanthropology and cognitive archaeology. Ultimately, understanding how chimpanzees acquire tool-use skills in social contexts may provide key insights into the origins of material culture and the processes that enabled its emergence. Finally, the dissertation concludes with a synthesis of the most significant results and a proposal for future research directions aimed at deepening the study of cultural evolution through primatology and cognitive archaeology.

2. THEORETICAL FRAMEWORK

2.1. Tool use in non-human primates

2.1.1. Capuchin monkeys

Capuchin monkeys have long been regarded as a valuable model in the study of animal culture, second only to great apes, due to their behavioural flexibility and certain parallels with humans. Several authors have emphasized their potential to explore how cultural traditions may arise and persist without the necessity of imitation or language. Van Schaik and Pradhan (2003) proposed an evolutionary model in which the emergence and maintenance of tool-use traditions in primates depend on three key factors: the probability of individual innovation, the capacity for socially biased learning, and the prevailing social conditions. Within this framework, high levels of sociability and social tolerance increase opportunities for the diffusion of skills within a group, enabling even species with moderate cognitive abilities to sustain complex behaviours once invented. This theoretical perspective is particularly relevant to capuchins, whose group living and propensity for object manipulation create a favourable context for the emergence of cultural traditions.

Empirical studies provide strong support for this view. Perry et al. (2003), based on more than a decade of observations in Costa Rica, identified several socially transmitted conventions in wild capuchins, many lacking any apparent adaptive function. Tool use in capuchins has been especially well documented in Brazil. Comparative research has shown that, while chimpanzees and capuchins both crack nuts using stone tools, capuchins display considerable individual variation: individuals select harder and heavier hammers for more resistant nuts, achieve success with fewer strikes, and obtain higher returns (Visalberghi et al., 2015). Similarly, Falótico et al. (2018) reported that hammer choice reflects adaptive selection, with repertoires varying across groups in ways that cannot be explained solely by ecological factors, pointing to the presence of cultural traditions. More recently, capuchins have been observed to accidentally produce sharp flakes during percussive activities, a finding proposed as a potential model for understanding the accidental origins of lithic technology in hominins (Luncz et al., 2022).

In addition, wild capuchin monkeys have been shown to unintentionally produce sharp flakes that closely resemble hominin-made tools, reinforcing the by-product hypothesis for the emergence of early lithic technology (Proffitt et al., 2016).

Observations from semi-captive settings further illustrate this capacity: capuchins cracked nuts using stones as hammers and anvils, frequently in the presence of infant and juvenile observers, thus providing opportunities for social learning (Ottoni & Mannu, 2001), and exhibit diverse tool-use behaviours that extend beyond basic foraging techniques, including manipulative actions such as pounding, rubbing, tapping, leaf-wrapping and other forms of object use (Panger et al., 2002).

Taken together, these findings show that capuchins combine technical skills, behavioural variability, and social transmission. Although less complex than great ape cultures, their tool use and social conventions illuminate the minimal conditions under which durable cultural traditions can arise and persist.

Figure 1. *Bearded capuchin (Sapajus libidinosus) using a stone hammer to crack nuts. Photo by L. Marino (Visalberghi et al., 2015).*

2.1.2. Macaques

Macaques are a diverse genus of old-world monkeys with broad geographic distribution and ecological variation. Although traditionally regarded as less sophisticated tool users than capuchins or chimpanzees, they provide important evidence for socially transmitted behaviours with cultural implications. The classic case described by Kawai (1965) on Japanese macaques (*Macaca fuscata*) remains one of the earliest demonstrations of cultural transmission in primates: a young female innovated potato-washing in seawater, a behaviour that spread gradually within the group, especially among younger individuals, and eventually became established as a stable local tradition. This pioneering study opened the way for systematic research on primate culture.

Subsequent work has revealed additional traditions. Stone handling, described by Huffman (1996), consists of repetitive and stereotyped manipulation of stones, transmitted socially and varying between groups. Later studies confirmed consistent differences in frequency and complexity across populations, reinforcing its interpretation as a cultural practice with primarily affiliative or playful functions (Nahallage & Huffman, 2008). Experimental research has further shown that Tonkean macaques (*Macaca tonkeana*) are capable of developing tool-use behaviours and extending them within social groups, although observers did not reproduce the actions of skilled demonstrators, suggesting that transmission relies mainly on individual learning rather than faithful imitation (Ducoing & Thierry, 2005). Finally, field experiments in Piak Nam Yai Island, Thailand, demonstrated that long-tailed macaques (*Macaca fascicularis aurea*) select stone tools of different masses depending on food type, such as lighter stones for attached oysters and heavier stones for larger unattached foods, providing strong evidence of adaptive tool selection in wild populations (Gumert & Malaivijitnond, 2013).

Overall, these studies demonstrate that macaques, although more limited in tool use than other primates, can sustain socially transmitted and enduring traditions, both playful and instrumental, thereby broadening our understanding of the scope and diversity of non-human culture.

Figure 2. *Japanese macaque (Macaca fuscata) washing sweet potatoes. Photo by T. Matsuzawa, 2008 (Matsuzawa & McGrew, 2008).*

2.1.3. Orangutans

Orangutans (*Pongo spp*.) represent a distinctive case among great apes due to their semi-solitary lifestyle and extended mother-infant bonds, which shape opportunities for social transmission. Despite being less habitual tool users in the wild compared with chimpanzees, they display a latent repertoire of technical abilities. One of the most compelling cases comes from Suaq Balimbing (Sumatra, Indonesia), where orangutans regularly employ modified sticks to obtain seeds or honey, preparing tools by stripping leaves or spines, whereas such behaviours are absent in other populations, indicating cultural variation rather than purely ecological necessity (van Schaik et al., 2003). These observations are consistent with theoretical predictions that the emergence and transmission of tool-use traditions in semi-solitary species such as orangutans rely primarily on vertical learning pathways, particularly the prolonged mother-offspring relationship (van Schaik & Pradhan, 2003).

Experimental studies have provided further evidence of orangutans' technical and cognitive sophistication. In a two-year longitudinal study of deferred imitation, conducted with enculturated apes at the Centre for Orangutan and Chimpanzee Conservation (Wauchula, Florida), orangutans successfully reproduced object-

manipulation tasks, with performance improving over time and reflecting representational abilities and memory processes (Bjorklund, Bering, & Ragan, 2000). Their skills also extend to structural innovation: orangutans have been observed modifying sticks, such as breaking or trimming them to suit specific tasks, providing evidence of flexible problem-solving and tool adjustment (Merrill, 2004).

More recently, naïve individuals have spontaneously engaged in stone tool use, including percussion and cutting, illustrating not only their capability to innovate complex tool behaviours without prior training but also the presence of latent solutions that can be expressed under favourable conditions (Motes-Rodrigo et al., 2022). Together, these findings underscore a robust cognitive substrate for flexible, adaptive problem-solving and provide important insights into the evolutionary roots of material culture in great apes. Recent perspectives have stressed the role of individual innovation in the emergence of tool use. Bandini (2021) argued that extended baseline periods, in which naïve individuals are provided with the necessary raw materials but no demonstrations, are crucial to determine whether behaviours can arise spontaneously. If behaviours emerge under these conditions, this indicates that individual learning, supported by non-copying social processes, is sufficient to explain their acquisition. From this perspective, many technical behaviours may arise as latent solutions under suitable ecological conditions and can later be stabilised and maintained through social learning.

With all, orangutans illustrate the interplay between individual learning and social transmission in ways that broaden our understanding of material culture. Although less frequent than in chimpanzees, their ability to manipulate, modify, and plan with objects demonstrates a cognitive substrate capable of sustaining local cultural traditions when ecological and developmental conditions are favourable.

Figure 3. *Juvenile male orangutan (Pongo abelii) performing spontaneous lithic percussion during an experimental condition (Motes-Rodrigo et al., 2022).*

2.1.4. Gorillas

Gorillas (*Gorilla gorilla*) have traditionally been considered the least technically proficient of the great apes, yet recent studies indicate that they possess a latent potential for tool-use behaviours, particularly when ecological or experimental conditions provide appropriate challenges. Their limited expression of tool use in the wild is better understood as a product of context rather than as evidence of cognitive incapacity.

Research in captivity has demonstrated that gorillas follow an ontogenetic progression of object manipulation that can culminate in basic instrumental actions. Bardo et al. (2017) examined manual actions in captive gorillas and found that they predominantly employed unimanual grips, but also displayed in-hand movements and, in one case, the interdigital brace posture. These findings suggest that gorillas possess considerable manual dexterity, capable of progressing from simple handling to more coordinated instrumental actions, with behaviours arising largely through individual exploration

rather than imitation. Nakamichi (1999) reported that young gorillas at the San Diego Wild Animal Park spontaneously used sticks as tools, including throwing them to knock down leaves and seeds, pulling branches, and beating foliage. They tended to select longer and thicker sticks for pulling and beating than for throwing, and in some cases inspected the target or even switched sticks when the first attempt failed. Notably, only the 8-year-old juveniles engaged in these behaviours, whereas adults and immatures did not, pointing to age-related differences in the expression of technical skills.

Evidence from wild populations further supports this view. Breuer et al. (2005) documented the first cases of tool use in wild western lowland gorillas, when two adult females employed branches in swamp habitats: one as a walking stick to test water depth and support locomotion, and another as both a stabiliser during feeding and as a self-made bridge. Unlike the feeding-related tool use typical of other apes, these observations underscore the role of ecological pressures, such as habitat challenges, as triggers for technical innovation. Laboratory work complements these findings: Byrne and Tanner (2006) showed that a zoo-housed female gorilla could spontaneously imitate several human-demonstrated gestures, such as slapping her cheek or swinging her arm, without training or rewards. Although the copies differed from the models, the authors concluded that gorillas, like other great apes, possess a latent capacity for gestural imitation.

In sum, current evidence shows that gorillas possess the cognitive and motor capacities required for instrumental behaviour, although these are expressed less frequently and with less complexity than in chimpanzees or orangutans. Factors such as low population density, a less tolerant social structure, and a non-extractive diet may restrict opportunities for social learning and reduce ecological necessity. Nevertheless, when developmental, environmental, or ecological conditions align, gorillas display a repertoire that reveals an unexpectedly rich technical potential. As such, they provide a valuable model for understanding how ecological and social contexts shape the expression of material culture among great apes.

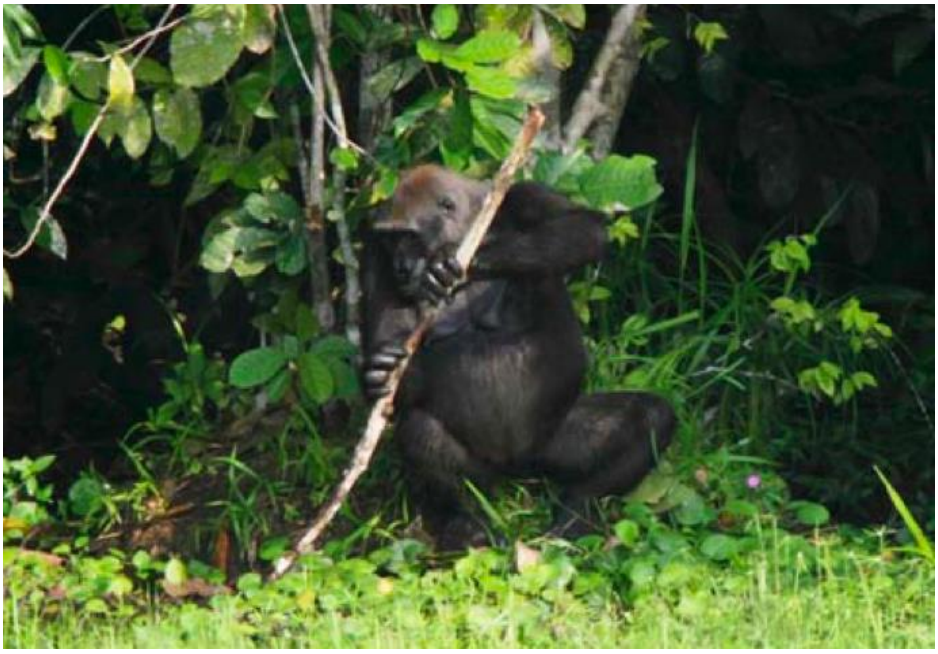


Figure 4. *Female western lowland gorilla (Gorilla gorilla gorilla) using a trunk as a stabiliser during food processing at Mbeli Bai (Breuer et al., 2005).*

2.1.5. Chimpanzees

Chimpanzees are the non-human species with the most extensive and diversified tool-use repertoire documented to date. Both in the wild and in captivity, they have exhibited a wide range of technical behaviours, with flexibility, innovation, and social transmission. This complexity has made chimpanzees the primary model for investigating the origins of material culture in hominins.

Boesch and Boesch (1990) documented the systematic use of stones as hammers and anvils in the Taï population (Côte d'Ivoire) to crack nuts. This technique entails selecting suitable materials and transporting both nuts and hammers to fixed anvils, with repeated strikes in a standardised sequence. These findings, together with cross-site contrasts, have been interpreted as population-level cultural traditions; transmission likely involves mother-offspring and within-group pathways (Whiten et al., 1999; Luncz & Boesch, 2014). Notably, chimpanzees at Gombe do not engage in nut-cracking with stones despite the local availability of stones, supports and hard-shelled fruits (Boesch & Boesch, 1990). Additionally, Pruetz and Bertolani (2007) reported at Fongoli (Senegal) the habitual use of sharpened stick tools, manufactured in multiple steps and used as spears, to hunt prosimian prey (lesser bushbabies), one of the few documented cases of tool-assisted vertebrate hunting in non-human primates.

Whiten et al. (1999) presented a systematic synthesis documenting 39 behaviour patterns that are customary or habitual in some African chimpanzee communities yet absent in others once ecological explanations were discounted. These include tool-use (e.g., termite-fishing and ant-fishing), grooming and body-care patterns (e.g., leaf-napkin, leaf-groom), courtship and attention-getting displays, and play invitations. The resulting cross-site variation is consistent with population-level traditions maintained through social learning, given that ecological and genetic factors were ruled out by the authors. More recently, Kühl et al. (2019) expanded this approach at a continental scale, demonstrating that chimpanzee behavioural diversity is significantly eroded by human impact, highlighting culture as not only an evolutionary feature but also a conservation target.

Several studies have examined mechanisms of acquisition. Nagell et al. (1993) argued that chimpanzees rely more on emulation than on faithful imitation of others' actions, whereas enculturated chimpanzees can show robust imitation under specific conditions (Tomasello et al., 1993a). Hirata et al. (2009), working with captive chimpanzees, demonstrated that individuals exposed to human or conspecific models using tools were more likely to acquire and reproduce the observed techniques, pointing to the role of visual demonstration and contextual enhancement.

Cultural transmission in chimpanzees is characterised by a combination of processes: vertical (mother-offspring), horizontal (between group members), and occasionally oblique (from adults to unrelated juveniles). Luncz and Boesch (2014) described cultural conservatism, in which new techniques, even when more efficient, are not easily adopted if they conflict with established practices. This phenomenon reinforces the normative character of some chimpanzee traditions. In this line, Whiten et al. (2009a) reviewed imitation-emulation dynamics in chimpanzees and children, showing that both species can sustain local traditions through social learning, yet chimpanzees exhibit relative conservatism and conformity, whereas humans display the copying fidelity that supports cumulative cultural complexity.

In controlled settings, chimpanzees have also demonstrated innovative capacities, such as modifying tools or combining them sequentially. Tonooka et al. (1997) documented

in captivity the emergence and social transmission of leaf-based drinking tools: individuals converged on *Thuja occidentalis*, learned by observing skilled users and re-using tools left by them, and performed a repeated action sequence (inserting, dipping, retrieving, licking); using Thuja required fewer actions than hand use, indicating technical efficiency. Moreover, Yamamoto et al. (2012) documented targeted instrumental helping, in which one individual spontaneously provided another with the necessary tool to complete a joint task.

Marked inter-individual differences have also been documented: some chimpanzees are more active in technical exploration, whereas others primarily learn by observing. Such variation may be influenced by age, sex, dominance rank, or personality. Marshall-Pescini and Whiten (2008a) suggested that cultural diffusion is shaped by opportunity to observe skilled models and individual predispositions, with motivational engagement likely modulating adoption.

Finally, some researchers such as Boesch (2012) have argued that chimpanzees possess an incipient form of cumulative culture, particularly in populations such as Taï, where technical improvements over time have been associated with intergenerational transmission. However, Tennie et al. (2009) contend that most chimpanzee behaviours can be explained as latent solutions, i.e., behaviours that individuals can rediscover independently given minimal social inputs, and that true cumulative culture is unique to humans. This contrast reflects a central debate in current primatology.

Overall, the study of tool-use behaviour in chimpanzees provides a fundamental basis for understanding the evolutionary prerequisites of technical and social culture, as well as the environmental and cognitive requirements that may have accompanied the earliest stages of cultural evolution in hominins.

Figure 5. *Female chimpanzee (Pan troglodytes) cracking Panda oleosa nuts with a stone hammer on a wooden anvil in Taï Forest (Proffitt et al., 2022).*

2.2. The Concept of Culture from a Scientific Perspective

The concept of culture has occupied a central role in disciplines such as anthropology, psychology, and evolutionary biology. Although all three share the aim of understanding how cultural practices emerge, are transmitted, and evolve, each discipline emphasises different facets of the phenomenon. Anthropology has traditionally considered culture as the hallmark of humankind, highlighting symbolism and language as its defining features. Psychology, by contrast, has investigated the cognitive and social mechanisms underpinning cultural transmission, focusing on the uniqueness of human cultural learning. Meanwhile, evolutionary biology has sought to establish general models of cultural origins and change, understanding culture as a parallel system of information transmission with its own evolutionary dynamics.

In order to situate the debate on primate cultures, and to establish the analytical framework for the present study, it is essential to review these three complementary perspectives. Each illuminates a different dimension of what culture is, how it operates, and why it matters in an evolutionary context.

2.2.1. An Anthropological Perspective

From an anthropological standpoint, culture has been classically regarded as an exclusively human domain, intimately bound to language, symbolism, and collective organisation. Holloway (1969), for instance, emphasised that culture must be defined not merely as learned behaviour but as socially transmitted practices capable of symbolic codification and cumulative development. In his view, non-human animals may display behavioural traditions, yet these lack the symbolic, normative and linguistic scaffolding that makes human culture unique. He argued that the emergence of culture was a qualitative evolutionary leap, underpinned by increased brain size, planning capacity, complex sociality, and the appearance of proto-symbolic communication. Once established, culture functioned as an autonomous system, capable of directing behaviour and even shaping biological evolution through processes of cultural selection. In this sense, anthropology historically tended to demarcate a sharp boundary between "true culture" in humans and the more limited social traditions of other species.

This anthropocentric view, however, has been increasingly challenged. Geertz (1973), though still writing firmly within an anthropological frame, highlighted that culture is not simply an add-on to biology but the very medium through which human beings exist as social and symbolic actors. His interpretive approach emphasised the role of meaning-making, rituals, and symbolic codes in organising human life, reinforcing the idea that culture cannot be reduced to technical skills or instrumental behaviour. Yet precisely this symbolic emphasis also left little room for recognising continuities with other species.

More recent anthropological contributions have sought to move beyond the human exceptionalist paradigm. Perry (2006), for example, argued for a functional rather than symbolic definition of culture, centred on socially transmitted information that persists over time and varies between groups. From this perspective, certain primate behaviours (such as nut-cracking in chimpanzees or ritualised greeting patterns in capuchins) can legitimately be considered cultural. Perry stressed that restricting the concept of culture to symbolism risks obscuring evolutionary continuities, whereas adopting a broader, functional definition allows us to situate human culture within a continuum.

Further, Perry (2009) explored the role of conformity in primate traditions, demonstrating how individuals tend to adopt behaviours that are frequent, successful, or socially tolerated within their groups. Such mechanisms provide stability to non-human primate traditions, even in the absence of symbolic scaffolding. This argument brings anthropology closer to a comparative stance, one that acknowledges gradations of culture rather than a strict human-animal dichotomy.

Taken together, these anthropological perspectives reveal a tension between two poles: one defending the uniqueness of human symbolic culture as Holloway or Geertz, and another proposing an expanded definition that incorporates non-human traditions, as Perry. This tension is central to the present study, which seeks to evaluate chimpanzee tool use not as a mere diluted reflection of human culture but as a cultural system in its own right, with distinctive mechanisms of transmission and persistence.

2.2.2. A Psychological Perspective

Psychological and cognitive approaches have examined culture primarily through the lens of social learning, asking how individuals acquire, transmit, and stabilise behavioural traditions. A key question has been whether the mechanisms that sustain culture in humans are qualitatively unique, or whether they represent elaborations of more general capacities shared with other primates.

A major focus has been the problem of imitation. Brass and Heyes (2005) highlighted the 'correspondence problem': how does the brain translate the perception of another's action into a matching motor representation? While specialist theories posit dedicated mechanisms for imitation, Brass and Heyes favoured a generalist account, pointing to the role of mirror neuron systems in premotor and parietal cortices, which activate both when performing and when observing an action. Importantly, they argued that these neural correspondences may not be innate but shaped through associative learning, meaning that the fidelity of imitation is itself culturally scaffolded. This argument establishes a bridge between neurocognitive processes and cultural transmission, showing how the brain can support imitation as a learned capacity.

Beyond imitation, humans possess mechanisms of pedagogical communication. Csibra and Gergely (2006) introduced the theory of "natural pedagogy," proposing that humans

are evolutionarily adapted to transfer and receive knowledge through teaching, via a dedicated communication system that does not presuppose language or theory of mind but may have facilitated their evolution. Later, Csibra and Gergely (2011) elaborated this hypothesis, showing that human infants are innately sensitive to ostensive cues, such as direct eye contact, infant-directed speech, or contingent reactivity, which they interpret as signals of teaching. This system enables the rapid and reliable transmission of cognitively opaque cultural knowledge, including ritual rules or symbolic codes that cannot be easily inferred from observation alone. Natural pedagogy thus represents an adaptation that uniquely underpins cumulative culture in our species, explaining why human traditions can achieve such depth and complexity.

Other psychological perspectives have emphasised the social motivation behind imitation. Over and Carpenter (2012) demonstrated that children copy actions with striking fidelity, even when causally irrelevant (so-called overimitation). They argued that this reflects not cognitive error but affiliative motivation: by imitating precisely, children signal group membership and social alignment. This highlights that cultural transmission is not only a matter of cognitive capacity but also of social belonging, with fidelity in copying serving both epistemic and social functions.

The broader theoretical synthesis is provided by Tomasello et al. (1999), who distinguished between emulation, imitation, and instruction as three forms of cultural learning. Humans, they argued, are characterised by "shared intentionality": the ability to recognise others' goals, align perspectives, and participate in joint activities. This capacity enables instruction, guided participation, and the accumulation of knowledge within shared cultural frameworks. By contrast, non-human primates may emulate or imitate to some degree but lack the intentional depth necessary for cumulative culture.

In sum, psychological perspectives emphasise the mechanisms of cultural transmission: from neural underpinnings of imitation, to innate pedagogical dispositions, to the social motivations for conformity and fidelity. They show how culture is not merely learned behaviour but the product of evolved cognitive architectures that support teaching, affiliation, and shared intentionality. These insights are crucial for situating primate traditions within a comparative framework: while apes demonstrate significant social

learning, the human capacity for pedagogy and shared intentionality appears to be a distinctive driver of cumulative culture.

2.2.3. A Biological Perspective

Biological approaches, often framed within the theory of dual inheritance, treat culture as a system of inheritance operating in parallel with genetic evolution and interacting with it. This perspective seeks to explain not only what culture is, but why it evolves, how it is maintained, and under what conditions it becomes cumulative.

The foundations of this approach were laid by Boyd and Richerson (1996), who distinguished between culture as social transmission of behaviour, common across many species, and cumulative cultural evolution, which is rare and largely unique to humans. Their mathematical models showed that while social learning can spread behaviours rapidly, only when combined with high-fidelity transmission and intergenerational stability does culture accumulate adaptively. Later, Boyd and Richerson (2005) highlighted the role of transmission biases, such as conformity (copying the majority) and prestige (copying successful or high-status individuals), as crucial filters that stabilise cultural traits and prevent their regression or degradation. These mechanisms ensure that traditions are not only maintained but also improved over generations, thereby supporting the cumulative dimension of human culture.

This critique was further developed by Enquist and Ghirlanda (2007), who stressed that social learning by itself is insufficient to explain cumulative culture. Instead, they argued that human cultural evolution requires selective mechanisms that allow useful innovations to persist while discarding maladaptive variants. Such mechanisms explain why only humans, and not other animals with social learning capacities, have developed the open-ended accumulation of cultural complexity.

Biological perspectives have also been enriched by more integrative frameworks. Fuentes (2016) advocated for the Extended Evolutionary Synthesis, in which culture is understood as part of the human niche. Within this perspective, and drawing on Niche Construction Theory, culture is not simply a product of evolution but an active force in shaping environments, behaviours, and selection pressures. Through niche construction, humans modify their ecological and social worlds in ways that feed back into genetic

and cultural evolution. This framework emphasises the inseparability of biology and culture, proposing a "biocultural" approach in which symbolic practices, ecological adaptations, and social dynamics jointly constitute the human evolutionary trajectory.

Finally, Whiten (2011) argued for a comparative view of culture across primates. He documented more than thirty cultural behaviours in chimpanzees, including tool use, social rituals, and communicative gestures. While acknowledging the absence of complex accumulation, Whiten stressed that chimpanzee traditions reveal the evolutionary roots of human culture, suggesting a gradient rather than a dichotomy. His work thus connects the biological and anthropological perspectives, emphasising both continuity and divergence.

In biological terms, then, culture can be seen as a system of inheritance and adaptation. It operates through social learning, is stabilised by cognitive biases, and interacts dynamically with ecological and genetic factors. The rarity of cumulative cultural evolution underscores the uniqueness of humans, but the presence of proto-cultural systems in primates highlights the evolutionary pathways that may have led to the emergence of human cultural complexity.

This synthesis shows that anthropology, psychology, and biology provide complementary accounts of culture. Anthropology highlights its symbolic and human-specific dimensions; psychology reveals the cognitive and social mechanisms enabling its transmission; and biology frames it as an evolutionary system in its own right. Taken together, these perspectives situate culture as both a uniquely human achievement and part of a broader continuum of social learning and tradition across species.

2.3. The First Studies of Culture in Non-Human Primates

For much of the twentieth century, the concept of culture was considered uniquely human, closely tied to symbolic meaning, language, and cumulative traditions. Kroeber and Kluckhohn's influential monograph *Culture: A Critical Review of Concepts and Definitions* (1952) systematized approximately 300 anthropological works and classified 164 definitions of culture into seven major conceptual categories: descriptive, historical, normative, psychological, structural, genetic, and incomplete, thereby

highlighting both the richness and the ambiguity of the term (Boroch, 2016). Against this background, the notion that non-human primates might also possess forms of culture appeared both controversial and provocative. Yet, from the 1950s onwards, a series of pioneering primatologists such as Kinji Imanishi, Jane Goodall, Dian Fossey, and Jordi Sabater Pi began to document behaviours in apes and monkeys that could only be explained through social transmission and tradition, rather than ecological necessity or genetic programming. Holloway (1969) further reinforced the prevailing anthropological view by arguing that culture should be regarded as a uniquely human domain, grounded in the symbolic and arbitrary imposition of meaning.

2.3.1. Kinji Imanishi

The Japanese primatologist Kinji Imanishi (1902-1992) is widely regarded as the first to propose that non-human animals might possess culture. Although his writings from the early 1950s remained largely unknown in Western academia for decades, later reviews recognised their pioneering nature and their challenge to anthropocentric assumptions about culture (de Waal, 2001; Matsuzawa & McGrew, 2008; Humle & Newton-Fisher, 2013).

Imanishi emphasised the importance of long-term fieldwork, which characterised the Japanese primatological tradition and distinguished it from Western ethology (Matsuzawa & McGrew, 2008; Humle & Newton-Fisher, 2013). His students' work on Koshima Island provided the first systematic description of socially transmitted behaviour in wild primates: the spread of sweet potato washing among Japanese macaques (Kawai, 1965). Originating with a juvenile female, this practice diffused through peers and kin, eventually becoming a group-wide tradition. Later analyses confirmed that it was not ecologically necessary and thus qualified as a cultural variant (Leca et al., 2007).

While initially overlooked outside Japan, Imanishi's perspective is now considered a foundational milestone in the scientific study of animal culture. His vision opened the door to conceiving primate behaviour not only in ecological or biological terms, but also as part of a continuum of tradition and culture shared with humans (de Waal, 2001; Matsuzawa & McGrew, 2008).

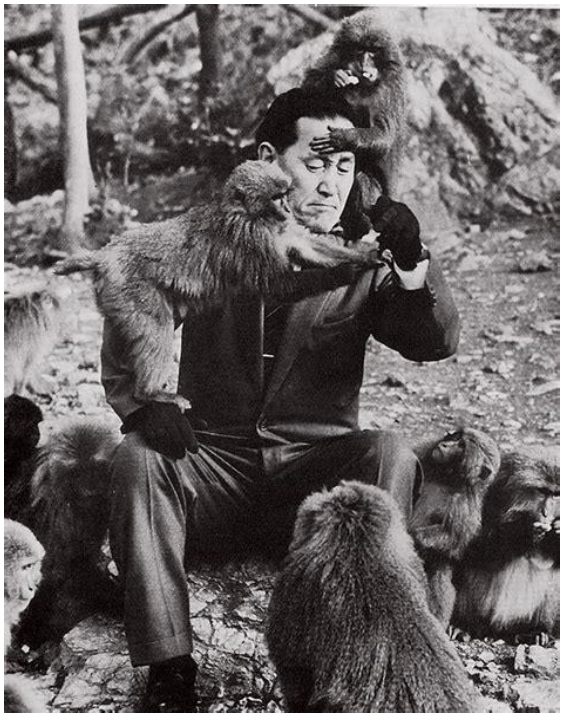


Figure 6. *Kinji Imanishi surrounded by Japanese macaques, circa 1963. Photograph from Monkeys and Apes Sociological Studies by Shunzo Kawamura & Junichiro Itani (Chukoron-Sha, Tokyo, 1965).*

2.3.2. Jane Goodall

A decade later, Jane Goodall's fieldwork at Gombe Stream, Tanzania, offered similarly revolutionary insights into chimpanzee behaviour. Beginning in 1960, Goodall adopted an ethnographic style of observation, assigning names to individuals, recording their life histories, and documenting their daily activities with unprecedented detail (Goodall, 1986).

Her early publications caused a sensation: in 1964 she reported tool use in termite-fishing, describing how chimpanzees stripped branches to insert them into termite mounds (Goodall, 1964). Later she documented aimed throwing, leaf-tool use, and a host of other techniques (Goodall, 1973). These findings shattered the then-dominant view, championed by anthropologists and philosophers, that humans alone were "man the tool-maker." As Laland and Galef (2009) observe, Goodall's discoveries became central to the debate on whether animal traditions can be regarded as cultural, even if they argue that such traditions are analogs rather than homologs of human culture.

Over the decades, Goodall's longitudinal data revealed not only behavioural complexity but also intra-species variability, with some behaviours present in certain chimpanzee communities but absent in others (Goodall, 1986). This suggested that chimpanzees possessed community-specific traditions, a notion later formalised in the cultural catalogues of Whiten et al. (1999). Her influence extended beyond the data: by treating chimpanzees as individuals with personalities, relationships, and histories, Goodall transformed primatology into a discipline attentive to social lives and cultures, inspiring generations of researchers.

Figure 7. *Jane Goodall observing chimpanzees in Gombe, Tanzania. Photograph by Michael Nichols, National Geographic Image Collection.*

2.3.3. Dian Fossey

In the 1970s, Dian Fossey established the Karisoke Research Centre in Rwanda to study mountain gorillas. Although she did not explicitly frame her work in terms of culture, her detailed observations revealed that gorillas possessed rich and structured social systems, with long-term bonds, dominance hierarchies, affiliative grooming, and play. Fossey meticulously documented the socialisation of young gorillas and the persistence of specific interaction patterns within groups (Fossey, 1983).

Her work had two lasting impacts. First, she transformed public perception of gorillas: from being depicted as aggressive brutes, they came to be seen as gentle, socially complex animals with family structures reminiscent of humans. Second, she provided a crucial empirical foundation for later scholars who considered whether certain gorilla

behaviours might qualify as traditions or cultural elements (Harcourt, 1996). Though Fossey herself did not advance a cultural framework, her work is now recognised as having broadened the scope of great ape studies to include social complexity as a precursor to culture.

Figure 8. *Dian Fossey interacting with mountain gorillas in Volcanoes National Park. Photograph by Robert I. M. Campbell, National Geographic Image Collection.*

2.3.4. Jordi Sabater Pi

In parallel to the Anglo-American and Japanese traditions, the Spanish primatologist Jordi Sabater Pi (1922-2009) played a crucial role in the development of cultural primatology. Working in Río Muni, Equatorial Guinea, Sabater Pi reported the use of leaf-sponges by chimpanzees to drink water, interpreting this behaviour as part of their material culture (Sabater Pi, 1974). This simple but effective technique, soaking a leaf and then squeezing the water into the mouth, was later included in Whiten et al.'s (1999) cultural catalogue as one of the best-documented examples of a chimpanzee tradition.

Beyond his discoveries, Sabater Pi made enduring contributions to the institutionalisation of primatology in Spain and Latin America, bridging primatology, anthropology, and ethnology. He emphasised the continuity between primate cultures and human prehistory, an idea that resonated with archaeological perspectives on the origins of material culture.

Figure 9. *Jordi Sabater Pi photographing a gorilla in Guinea, 1960s (date unknown). Source: Sabater Pi Collection, Universitat de Barcelona.*

Taken together, the contributions of Imanishi, Goodall, Fossey, and Sabater Pi represent the formative period of cultural primatology. They introduced new methodologies, ranging from long-term ethnography to detailed individual-based observation, and produced empirical evidence that social learning and tradition shape primate behaviour. Their work shifted the study of non-human primates from a focus on ecology and biology towards a recognition of culture as an evolutionary phenomenon.

These pioneering studies also sparked debates that continue today: to what extent do primate traditions resemble human culture, and how should culture be defined across species?

By establishing the legitimacy of the question itself, these early primatologists opened the door to subsequent developments, including the large-scale ethnographic surveys of Whiten et al. (1999) and the experimental paradigms that now dominate cultural primatology (Horner & Whiten, 2005; Marshall-Pescini & Whiten, 2008b). Their legacy endures as a reminder that the boundaries of culture are not uniquely human, but part of a continuum across the primate order.

2.4. The Study of Culture in Primates: Wild vs. Captivity

2.4.1. Studies in the Wild: Ecological Validity and Limitations

The study of culture in non-human primates in the wild has been crucial for demonstrating the existence of socially transmitted traditions. The pioneering observations of Goodall (1964, 1973, 1986) at Gombe revealed for the first time tool use in free-living chimpanzees, showing that communities can develop their own repertoires. In Taï Forest, Boesch and Boesch (1990) and Boesch et al. (1994) described in detail nut-cracking, a skill that requires prolonged learning and varies between communities, consolidating the notion of "wild cultures" (Boesch, 1995, 1996, 2012).

This line of research was extended by the comparative surveys of Whiten et al. (1999, 2001), which identified more than 30 cultural behaviours across chimpanzee populations in Africa. These studies showed that many practices cannot be explained solely by ecology but depend on social transmission. Other field studies have explored the development of such skills: Inoue-Nakamura and Matsuzawa (1997) showed how young chimpanzees in Bossou learn nut-cracking through trial-and-error sequences, while Sugiyama and Koman (1979) and Watts (2008) described local tool-use practices in Guinea and Uganda. At a comparative scale, Luncz et al. (2012) and Lycett et al. (2007) provided evidence of cultural differences even between neighbouring communities. In parallel, Yamakoshi (2001) highlighted the importance of ecological context, but also the need for social transmission to stabilise practices such as nut cracking.

Despite these advances, wild studies face limitations. Naturalistic observation provides unique ecological validity, yet the lack of experimental control makes it difficult to establish causal links between innovation and social learning (Huffman & Hirata, 2003). Furthermore, the low frequency of certain behaviours, small sample sizes, and the difficulty of following individuals over long periods complicate systematic analyses.

In recent years, research has shown that the study of primate culture continues to evolve. Izar et al. (2025) emphasises the need to integrate cultural diversity into conservation strategies, since fewer than 3% of primate species have been studied in this regard. Recent studies have broadened the focus beyond tool use. Malherbe et al. (2025) provide compelling evidence of culturally distinct gestural signals in wild chimpanzees,

some of which disappear following demographic decline, thereby illustrating both innovation and cultural loss. In parallel, Westra et al. (2024) propose a structured framework for investigating normative regularities in non-human primates, laying the theoretical groundwork for the empirical study of social norms. At the same time, technological innovations are transforming methodologies: the use of drones has generated large-scale datasets on baboons (Duporge et al., 2025) and computer vision has enhanced the recognition of chimpanzee social behaviour (Ma et al., 2024).

Overall, field studies have been essential in demonstrating that culture is not exclusive to humans. Despite their limitations, they continue to offer an irreplaceable perspective on primate cultural repertoires, and the incorporation of new methodologies ensures that this field remains central to research on the origins of culture.

2.4.2. Studies in Captivity: Process Control

Captive studies have been central to understanding the cognitive and social mechanisms of culture in primates. Unlike fieldwork, experimental settings allow for variable control, replication of conditions, and detailed access to individual-level data, all of which are essential for identifying the processes underlying cultural transmission.

One of the most influential areas has been the study of imitation and emulation. Tomasello et al. (1987, 1993a, 1993b, 2005) developed paradigms to distinguish between copying actions and copying results, showing that chimpanzees often prefer emulation strategies, although they may imitate in specific contexts. In enculturated individuals raised in close contact with humans, the tendency towards faithful imitation is more pronounced (Custance et al., 1995; Carrasco et al., 2009), highlighting the influence of social environment on learning strategies.

Other research has explored instrumental rationality and flexible information use. Buttelmann et al. (2007, 2008) demonstrated that chimpanzees can select more efficient options depending on context, while studies such as Hopper et al. (2008), using “ghost” conditions, revealed that they are capable of learning even without a visible model. In parallel, experiments on lithic tool manufacture and use with bonobos and chimpanzees (Toth et al., 1993, 2006; Schick et al., 1999) have established direct connections with

early hominin technologies, suggesting that captive research can illuminate evolutionary processes.

More recently, studies have moved beyond simple actions to investigate complex behaviours such as sequential tool use (tool sets). Bernstein-Kurtycz et al. (2020) showed that a group of zoo-housed chimpanzees could spontaneously use tools in the correct order, suggesting that this behaviour falls within their Zone of Latent Solutions (ZLS). However, the behaviour did not stabilise across sessions, indicating that social and ecological factors present in the wild may be required to sustain it.

New methodologies have further expanded the potential of captive research. Laumer et al. (2025) compared orangutans in the wild and in zoos, finding that captive individuals displayed greater diversity in exploratory object manipulations, revealing cognitive potential that is difficult to detect in natural settings. Complementarily, Splinter et al. (2025) showed that wild individuals can outperform captive ones in specific problem-solving tasks, underlining the role of ecological context. At the same time, advances in artificial intelligence and computer vision are transforming experimental approaches: the AlphaChimp system (Ma et al., 2024) substantially improves the recognition of social behaviours in video, while platforms such as LabGym (Ardoin & Sueur, 2023) allow automatic identification of complex manipulations. These tools provide unprecedented opportunities for systematic analysis in experimental settings.

Despite these undeniable contributions, captive studies also face important limitations. Human presence and artificial environments may alter behaviour (Tomasello, 1999), and the typically small group sizes limit generalisation. Nevertheless, controlled experimentation remains indispensable for testing hypotheses about cultural transmission and instrumental cognition. In combination with new technologies, captive research not only continues to provide fundamental insights into social learning processes but also stands as a key tool for understanding the nature and boundaries of primate culture.

2.4.3. Complementarity Between the Two Approaches

The study of culture in non-human primates requires the integration of data from both field and captive research, as each provides complementary strengths and limitations.

Field studies ensure ecological validity, allowing researchers to observe how cultural behaviours emerge, are maintained, and are transmitted in natural conditions. This has been crucial for documenting the diversity of chimpanzee and primate traditions (Whiten et al., 1999; Boesch, 2012; Perry, 2006). Yet the difficulties of establishing causal relationships and controlling environmental variables highlight the need for experimental approaches.

Captive studies, in turn, provide process control, enabling the testing of hypotheses on learning mechanisms under replicable conditions. These studies have been decisive in exploring the distinction between imitation and emulation (Tomasello et al., 1993a; Hopper et al., 2008), instrumental rationality (Buttelmann et al., 2007), and sequential tool use (Bernstein-Kurtycz et al., 2020). With the rise of new technologies, such as automated behaviour recognition systems (Ma et al., 2024; Ardoin & Sueur, 2023), captive research has become even more precise and scalable.

Complementarity lies in the fact that fieldwork shows what primates actually do in their natural habitats, while captivity allows us to explore how and why they acquire these behaviours. Authors such as Boesch & Tomasello (1998) and Whiten (2011, 2017c) have argued that only by combining both approaches can the complexity of cultural phenomena be fully understood. In this sense, recent comparisons between wild and captive individuals (Laumer et al., 2025; Splinter et al., 2025) reinforce the idea that ecological origin strongly shapes behavioural repertoires, while underlying cognitive potential can be revealed in controlled contexts.

In sum, integrating both approaches provides a more complete and nuanced understanding of primate culture, and constitutes an indispensable model for approaching the origins and evolution of human culture.

2.5. Methodologies for the Study of Culture and Social Learning in Primates

2.5.1. The Ethnographic Method in Non-Human Primates

The ethnographic method applied to non-human primates consists of identifying and comparing group-level behavioural variants that cannot be explained by ecological or genetic differences, thereby inferring the existence of traditions or culture (Whiten et

al., 1999, 2001). Within this framework, culture is operationalised as behavioural repertoires that exhibit stable geographical variation and plausible social transmission, using a method of exclusion and inter-site comparisons to rule out alternative explanations.

This approach has documented marked cultural differences between neighbouring chimpanzee communities despite female migration, suggesting the persistence of local traditions (Luncz et al., 2012; Luncz & Boesch, 2014, 2015). Comparative catalogues have mapped a wide diversity of practices (e.g., tool percussive behaviours, termite-fishing, communicative acts) and characterised their regional distribution (Whiten et al., 1999, 2001). Such evidence has also proved relevant to conservation, as anthropogenic pressures can erode behavioural diversity (Kühl et al., 2019) and promote cultural change as a flexible response to human disturbance (Gruber et al., 2019).

The strengths of the ethnographic method include its high ecological validity, extensive temporal and spatial coverage, and its capacity to describe population-level cultural patterns. Nevertheless, it remains largely correlational, limiting the ability to identify specific learning mechanisms. This underscores the need to complement ethnography with experimental approaches.

2.5.2. Experimental Studies in Captivity: Diffusion and Cognition

Experimental studies in captivity allow for greater control of variables and the causal testing of transmission mechanisms (Hoppitt & Laland, 2013). Research in this domain has developed along two principal lines: social diffusion studies and cognitive studies.

2.5.2.1. Social Diffusion Studies

Diffusion studies introduce a novel technique to one individual or subgroup and track its spread across the wider community (Whiten et al., 2005). Using paradigms such as diffusion chains, researchers have demonstrated that chimpanzees can maintain and copy traditions in controlled settings (Horner et al., 2006; Hopper et al., 2010).

Classic examples include puzzle box experiments, where different solutions spread within a group depending on the initial model, providing evidence of transmission fidelity and conformity (Whiten et al., 2005; Hopper et al., 2008). Indeed, controlled

experiments have even shown the spread of arbitrary conventions within groups (Bonnie et al., 2006), reinforcing the centrality of social learning in cultural transmission. Collectively, such studies laid the foundation for an experimental science of animal culture (Mesoudi & Whiten, 2008).

2.5.2.2. Cognitive Studies

Cognitive studies focus on the psychological mechanisms underlying social learning and cultural transmission. Comparative experiments with human children and chimpanzees revealed key differences between action imitation and goal emulation, with humans showing a greater tendency towards high-fidelity copying (Tomasello et al., 1993a, 1993b; Nagell et al., 1993). Other work has examined the role of rationality in imitation (Buttelmann et al., 2007, 2008), the distinction between automatic and intentional mechanisms (Brass & Heyes, 2005), and the proposal of a natural pedagogy system facilitating cultural learning (Csibra & Gergely, 2006, 2011).

Recent reviews highlight that non-human primates rely on a combination of mechanisms such as observation, social reinforcement, emulation, and selective copying; however, the high-fidelity imitation required for cumulative culture remains rare (Heyes, 2011). This points to the importance of considering multiple interacting processes and their dependence on social and ecological contexts.

2.5.3. Importance of Complementarity

The combined use of the ethnographic method in the field and experimental approaches is essential for advancing our understanding of culture in primates. Ethnographic data provide ecological validity and contextual diversity, while experimental studies allow for the isolation of causal mechanisms (Whiten, 2017a; Kendal et al., 2018).

Recent frameworks also show that opportunities for social learning are shaped by social structure, levels of tolerance, hierarchy, and model availability, which directly affect transmission (van Boekholt et al., 2021). In parallel, novel quantitative tools such as network-based diffusion analysis (Franz & Nunn, 2009) and multilayer network modelling (Finn et al., 2019) offer innovative means of integrating ecological, social, and cultural dimensions within a single framework.

In sum, the complementarity of ethnographic and experimental approaches enables researchers to evaluate both the patterns and the underlying mechanisms of cultural transmission and is fundamental to assessing the continuities and differences between human and non-human primate cultures (Whiten, 2021).

2.6. Cumulative culture

Chimpanzees present the broadest ethnographic profile of cultural variants observed in non-human primates (Whiten et al., 1999). These behavioural differences across communities are generally regarded as cultural, since they cannot be fully explained by ecological or genetic variation. However, many of these traits are not socially dependent in a strict sense: individuals are often capable of re-innovating them independently when provided with favourable conditions in captivity (Tennie et al., 2009). For example, tool use for food extraction can readily emerge without direct social transmission. In such cases, social learning primarily serves to stabilize and spread the behaviour within the group, rather than being essential for its acquisition (Whiten et al., 2009b; Tennie et al., 2009).

This distinction highlights the difference between ordinary cultural traits and cumulative culture. Cumulative culture, often described as the hallmark of human cultural evolution (Tomasello, 1999; Tennie et al., 2009), refers to behaviours that are culturally dependent in a way that no individual could re-invent them alone. Human societies are the product of faithful accumulation of incremental innovations across generations, the so-called "ratchet effect" (Tomasello et al., 1993a; Tennie et al., 2009).

The key controversy in contemporary debates is whether non-human animals also exhibit cumulative culture. While earlier discussions focused on whether a behaviour was cultural at all, the current question is whether any non-human traits meet the criteria for cumulative cultural evolution (Dean et al., 2013; Mesoudi & Thornton, 2018). In the wild, only a handful of candidates have been proposed, typically behaviours requiring multiple steps or tool sequences. Among chimpanzees, the best-documented example comes from the Goualougo Triangle (Republic of Congo), where individuals employ up to three or four tools in sequence to exploit different types of termite nests, forming complex "tool kits" (Sanz & Morgan, 2007; Sanz et al., 2009). Such multi-step tool use

appears unlikely to be reinvented individually and may represent a case of cumulative cultural evolution. Other potential examples include nut cracking in West African chimpanzees (Boesch & Boesch, 1984; Whiten et al., 2009b).

In captivity, however, the evaluation of cumulative culture remains scarce. Our study contributes to this discussion by assessing chimpanzees' ability to employ tool sequences in a novel context, thereby testing the extent to which cumulative cultural traits can emerge and stabilize beyond the wild.

3. MATERIALS

3.1. Study site

The present study was conducted at Fundació Mona (www.fundacionmona.org), a rescue, rehabilitation, and research centre for non-human primates located in the municipality of Riudellots de la Selva, in the eastern part of the Selva region (Girona province, Catalonia, Spain), approximately 12 km south of the city of Girona (41º54'N, 2º49'E; UTM: 484933, 4639074). The centre covers an area of approximately 5 hectares. The local climate is coastal Mediterranean, characterized by hot, dry summers and mild winters, and the dominant vegetation is Mediterranean woodland and riparian forest.

Since its establishment in 2000, Fundació Mona's main objectives have been the rescue and rehabilitation of non-human primates confiscated from illegal trade or private ownership, their physical and psychological recovery, integration into stable social groups, and the promotion of their welfare. The foundation is a non-profit organization and adheres to the basic principles of a sanctuary: it does not engage in captive breeding or commercial exploitation of animals, and it does not allow direct contact between the public and the primates.

Figure 10. *Satellite image of the grounds of the Fundació Mona Primate Rescue Centre processed by ICGC (n.d.), under CC BY 4.0 licence*.

The main facilities include a naturalized outdoor enclosure of 5,640 m², divided into two areas (2,420 m² and 3,220 m²) separated by an internal barrier. The perimeter consists of a double security fence: a steel mesh and a 12-volt electrified fence, separated by approximately 25 cm. The outdoor area contains Mediterranean and riparian vegetation, as well as various wooden structures, towers, ropes, and artificial termite mounds that serve as environmental and cognitive enrichment. In addition, the enclosure has observation points designed to minimize interference with the animals' behaviour during observation and recording sessions.

The indoor dormitory (140 m²) is directly connected to the outdoor enclosure and is used to house the chimpanzees overnight or during periods of adverse weather conditions. Access between the indoor and outdoor areas is provided through tunnels, which remain open most of the time except during maintenance or cleaning tasks. For the purposes of this study, the experimental sessions were carried out inside the tunnels connecting the dormitory to the outdoor enclosure. This location allowed for full control over the development of the task, ensuring continuous visibility of the subjects and the possibility of starting sessions at the exact desired moment. Furthermore, this configuration facilitated the manipulation of the experimental devices and reduced interference from external stimuli, thereby ensuring optimal conditions for observation and data collection.

Figure 11. *Experimental tunnel used during the study. On the left, the outdoor enclosure where the chimpanzees spend the day; on the right, the indoor holding rooms. In the foreground, the camera used to record the sessions is visible.*

3.2. Subjects

A total of ten chimpanzees (*Pan troglodytes*), aged approximately between 25 and 45 years during the experimental phase, were evaluated in this study. The sample included individuals from different subspecies (*Pan troglodytes troglodytes, Pan troglodytes verus, Pan troglodytes ellioti,* and hybrids), housed at Fundació Mona (Riudellots de la Selva, Girona).

Most individuals originated from highly humanized environments, including use for commercial purposes (circus performances, television programs, and advertising), zoos, and private collections. In these contexts, many had been prematurely separated from their mothers and deprived of contact with conspecifics, growing up under deficient social and physical conditions.

Upon arrival at Fundació Mona, all individuals undergo a standardized resocialization protocol with three main objectives:

1. To reduce dependency on, and demand for, human interaction.
2. To facilitate intraspecific socialization, promoting contact with conspecifics.
3. To encourage species-typical behaviours and reduce abnormal behaviours derived from isolation or chronic stress.

At present, the individuals included in this study are organized into two stable social groups: Bilinga and Mutamba. Both groups spend most of the day in the outdoor naturalized enclosure and have access to indoor areas and socialization areas. The composition and life histories of the individuals in each group are described below.

3.2.1. Bilinga

The Bilinga group is named after *Nauclea diderrichii*, a tree native to Central and West Africa, typically found in lowland tropical and subtropical moist forests, currently threatened by intensive logging. This species produces fruits highly appreciated by chimpanzees (*Pan troglodytes*), to the extent that specific vocalizations associated with their location in the wild have been documented (Kalan et al., 2015).

At the time of the study, the Bilinga group was composed of five individuals: three males (Nico, Tom, and Víctor) and two females (Cheeta and Coco), belonging to

different *Pan troglodytes* subspecies. Individuals ranged in age from approximately 25 to 45 years, with diverse backgrounds, most of them related to captivity and previous use in performances, as pets, or in zoos.

Cheeta spent nearly three decades in a zoo before arriving at Mona. She is a large-sized female, and displays notable social skills, especially with Coco. Coco was illegally acquired as an infant and kept as a pet until her rescue. She is a well-balanced and very sociable individual. Nico arrived at Mona at the age of three with severe health problems derived from his past in television shows. He is the first non-human primate diagnosed with Chiari malformation and, despite physical sequelae such as partial finger amputation, maintains an active social life (Solis-Moruno et al., 2017). Tom, from a circus background, has a more nervous disposition but has successfully adapted to the group, where he partially assumes leadership functions. Finally, Víctor lived in isolation for 24 years before being rescued in France.

The social dynamics of the Bilinga group are characterised by a loosely defined hierarchy, with generally positive interactions. Although Tom can assume leadership roles and Nico exhibits dominance potential, neither maintains stable control. The group displays high levels of affiliation, with frequent grooming and play, and a low incidence of serious conflicts (Chen et al., 2024).

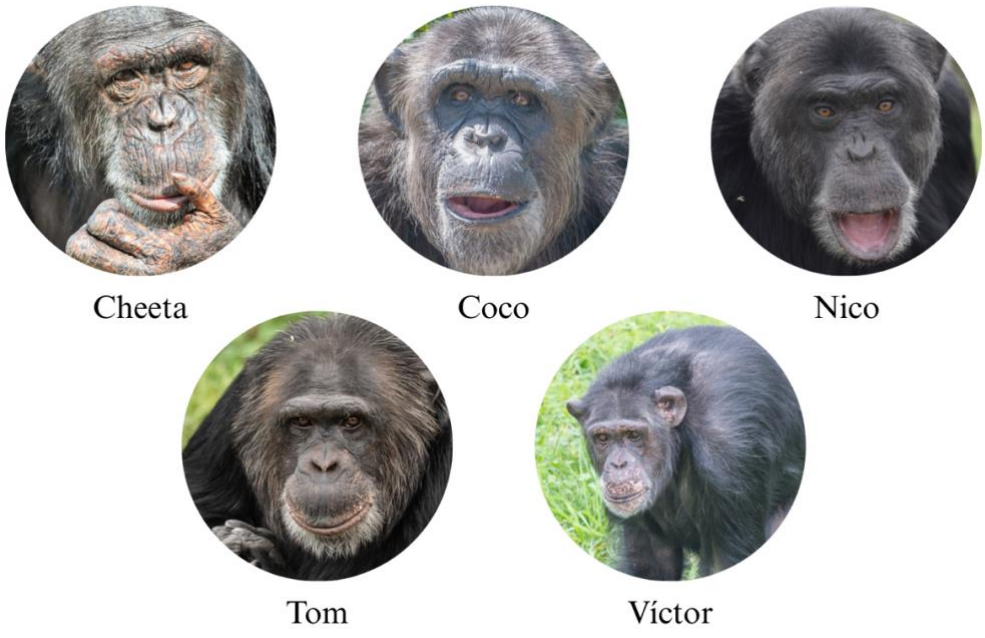


Figure 12. *Members of the Bilinga group (five chimpanzees included in the study). Images courtesy of Fundación Mona (https://fundacionmona.org).*

3.2.2. Mutamba

The Mutamba group is named after *Strychnos spinosa*, a tree native to tropical and subtropical Africa which, after the rainy season, produces a yellow, bittersweet, and highly nutritious fruit consumed by both humans and various animal species, including primates.

At the time of the study, the Mutamba group was composed of five individuals: three males (Bongo, Juanito, and Marco) and two females (Àfrica and Waty), belonging to different *Pan troglodytes* subspecies. Their ages ranged approximately between 22 and 41 years, with diverse origins, mostly associated with captivity and prior use in performances, as pets, or in zoos.

Àfrica was captured as an infant in the wild and illegally introduced into Spain. She suffered from severe stress and integration difficulties, but she is now a socially skilled female, with notable dexterity in tool-use tasks. Bongo, also from a circus background. He eventually displaced the former group leader and currently serves as the alpha male, although still consolidating a balanced leadership. Juanito was confiscated from a zoo where he had been prematurely separated from his mother. He formed a strong bond with Waty and has become a robust adult, actively engaged in group life. Marco was one of the first individuals rescued by Fundació Mona, previously featured in advertisements and shows. Despite suffering from chronic heart disease, he remains a key element of the group's social cohesion. Waty, with a background in the entertainment industry, displays great social intelligence and maintains a strong bond with Àfrica.

The social dynamics of the Mutamba group show a more clearly defined hierarchy compared to Bilinga, with Bongo as the current leader. Affiliative relationships are frequent, particularly among the females, and social cohesion is high, although disputes can occur in competitive contexts, such as access to resources or intergroup interactions.

Figure 13. *Members of the Mutamba group (five chimpanzees included in the study). Images courtesy of Fundación Mona (https://fundacionmona.org).*

Name	***Sex***	***Year of Birth (approx.)***	***Subspecies***	***Origin and location***	***Social Group***
Àfrica	F	1997 - 1999	*P. t. verus*	Wild - West Africa	Mutamba
Bongo	M	2000	*P. t. troglodytes* × *P. t. verus*	Captivity - Valencia	Mutamba
Cheeta	F	1986	*P. t. verus*	Wild - Liberia / Ivory Coast	Bilinga
Coco	F	1990	*P. t. troglodytes*	Wild - Equatorial Guinea	Bilinga
Juanito	M	2003	*P. t. troglodytes* × *P. t. verus*	Captivity - Tenerife	Mutamba
Marco	M	1984	*P. t. troglodytes*	Captivity - Valencia	Mutamba
Nico	M	2000	*P. t. troglodytes*	Captivity - Valencia	Bilinga
Tom	M	1980	*P. t. ellioti*	Possibly wild - Cameroon	Bilinga
Víctor	M	1982	*P. t. troglodytes* × *P. t. verus*	Captivity - France	Bilinga
Waty	F	1996	*P. t. troglodytes* × *P. t. verus*	Captivity - Valencia	Mutamba

Table 1. *Demographic information of the individual chimpanzees from the Bilinga and Mutamba groups, including name, sex, age, subspecies, origin, and social group.*

Note. M = male; F = female; *P. t. troglodytes* = *Pan troglodytes troglodytes*

3.3. Materials

3.3.1. Tools

Chimpanzees were provided with two different types of tools: rigid and flexible. All tools consisted of natural bamboo branches (*Bambusoideae*) sourced from plantations within the facilities of Fundació Mona, which are regularly cultivated for enrichment purposes. The branches were cut specifically for the experiment and prepared according to the requirements of the task.

Rigid tools measured approximately 20-25 cm in length and had an average diameter of about 1 cm, whereas flexible tools measured between 60-70 cm in length and had a diameter below 0.3 cm. These dimensions were established to ensure a clear functional distinction between the two types.

In each experimental session, a total of 20 tools (10 rigid and 10 flexible) were provided, placed either inside the tunnel or in its immediate surroundings (at the entrance or on the external structure of the tunnel).

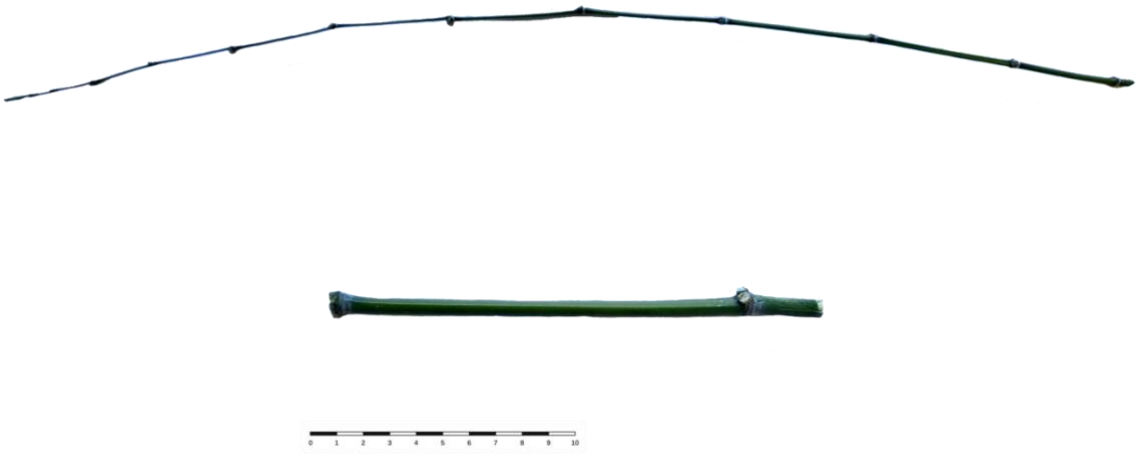


Figure 14. *Tools provided to chimpanzees during the experiment. The flexible tool (top) and the rigid tool (bottom), both were prepared from natural bamboo branches (Bambusoideae).*

3.3.2. Experimental devices

The experimental device, adapted from the design described by Bernstein-Kurtycz et al. (2020), consisted of a plastic tube of approximately 40 cm in length and 2.5 cm in diameter. Its morphology included a downward curve in the last 10-12 cm, where the

food reward was deposited. At the distal end, a removable cap allowed for both the introduction of the reward and cleaning of the device at the end of each session.

Although the tube had only one access opening, the task was not straightforward. Retrieving the reward required sequential tool use. At approximately 15 cm from the opening, a folded piece of baking paper (three layers) was inserted as a barrier to create resistance. This barrier could only be pierced with the short, rigid branch. Subsequently, the subject had to insert the longer, flexible tool, as the curvature of the tube prevented access to the reward with the rigid tool.

The device was installed using a metal plate fixed to the mesh of the tunnel, which allowed the tube to be screwed in and easily removed for preparation and cleaning. The dimensions of the opening prevented direct hand access, so chimpanzees could only manipulate it externally or insert a finger for exploration or inspection.

No visual markings or external cues were added to avoid artificial stimuli that could divert attention from the task. In each session, two devices were used simultaneously, placed independently within the experimental area.

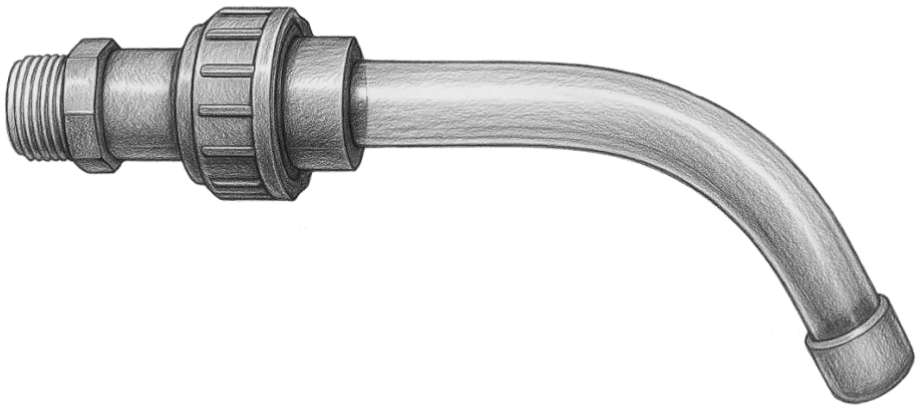


Figure 15. *Schematic representation of the experimental device used in the tool-use tasks. The curved plastic tube (40 cm × 2.5 cm) contained a paper barrier and a food reward at the distal end.*

3.3.3. Food reward

As an incentive for completing the experimental task, fruit purées made of apple and banana (*Anela Hop* brand) were used. These products consist exclusively of 100% natural fruit, with no added sugars or additives, thus meeting the necessary safety and health criteria for the welfare of the subjects.

The total amount administered per session was 100 g, distributed equally between the two experimental devices (50 g each). The reward was always placed at the end of the tube, behind the paper barrier, ensuring that it could only be accessed through the correct use of the tools. Additionally, a small amount of purée was placed at the entrance of the tube to attract the chimpanzees' attention and motivate them to interact with the device.

Selection criteria for the reward ensured that it was highly attractive and palatable to the individuals, easily retrievable with the flexible tool, and at the same time healthy. The same reward was used in all sessions to avoid variations in motivation or attractiveness, and less suitable products for their diet, such as processed sauces (e.g., ketchup), which have been used as incentives in other studies, were deliberately excluded.

3.3.4. Recording system

All experimental sessions were video-recorded using a GoPro Hero 4 camera placed at a fixed point approximately 1-1.5 m away from the experimental tunnel (see **Figure 11**). The camera was fixed on a specifically designed structure to ensure stability and a consistent perspective across sessions. A wide-angle setting was used to maximize visibility of both the subjects and the device. Each session lasted 30 minutes, with a total of 15 sessions per group (30 sessions in total).

Data recording was carried out continuously throughout each session, at the individual level, coding both interactions with the device and other relevant behaviours such as inspections and insertions (see **Table 2**).

Behavioural coding followed an ethogram (see **Table 2**) specifically designed for this study, and data were later transcribed and analysed using Excel spreadsheets. The

ethogram included operationally defined behavioural categories to ensure consistency and replicability of the data collection.

Variable	*Description*	*Categories / Examples*
Session	Session identifier	e.g., S13BI9_06
Group	Social group	Bilinga (BI); Mutamba (MU)
Subject	Individual chimpanzee	Àfrica (AF), Bea (BE), …, Waty (WA)
Sex	Sex of subject	Male (M); Female (F)
Age	Approximate age of subject	In years
Hole	Position of the artificial mound hole used	1: closest to the bedrooms; 2: facing the outdoor enclosure
Start time	Start time of tool-use attempt	Minutes:Seconds (e.g., 02:42)
End time	End time of attempt	Minutes:Seconds (e.g., 03:03)
Total duration	Duration of the tool-use attempt	Minutes:Seconds (e.g., 00:21)
Enrichment	Type of enrichment used	Individual; Social
Secondary subjects	Another chimpanzee involved	Same codes as Subject
Inspection	Chimpanzee inspection of the device without tool insertion, using hands, mouth or tool	Manual; Mouth; Tool
Interaction	Chimpanzee interaction with the device using hands, mouth or tool	Manual; Mouth; Tool
Tool	Tool type used by the chimpanzees. Could be rigid or flexible	Rigid; Flexible
Dip	Chimpanzee insertion of the tool into the device. Dips could be successful or failures	Success: Tool extracted with food reward. Each successful dip implied the cellophane barrier had been pierced. Failure: Tool inserted but no reward obtained. Determined via transparent tube. Includes attempts with rigid tools that could not reach the food.

Sample	Chimpanzee inserted tool into mouth for one to three seconds	Yes; No
Tool modification	Chimpanzee modified tool, using either their mouth or hands. This could be any of the two tool types	Chew; Bend; Break
Tool set	Use of multiple tools for a single goal	Yes; No
Tool sequence	A tool-set sequence defined as ≥1 dip with a rigid tool followed by ≥1 dip with flexible tools	Yes; No
Tool transported	Whether tool was carried from elsewhere	Yes; No
Tool transferred	Type of tool transfer between individuals	Active, Passive, Hesitant, Refusal, Possession change, Unknown; Proactive, Tolerated take, Steal, Failed steal, Failed attempt

Table 2. *Ethogram of tool-use behaviours and associated categories used for data coding in the study.*

4. METHODS

4.1. Study design

The study followed both an experimental and an observational design. It was experimental because a novel, complex two-step task requiring the sequential use of tools was introduced; and observational because chimpanzee behaviour was recorded through video footage and subsequently coded in detail.

The main aim of the design was to characterize the development and variability in tool use, analysing both success in reward extraction and the associated exploration patterns, and technical behaviours involved (e.g., tool transport or modification).

The basic unit of analysis was the individual interaction with the experimental device (insertions, inspections, and extraction attempts). However, the study was structured at two levels: (1) the individual level, to assess each subject's ability to solve the task; and (2) the group level, to examine the social dynamics associated with the task, such as tool transfer or potential processes of social learning.

The temporal design was longitudinal, as behaviour was monitored across 15 sessions per group (30 in total), each lasting 30 minutes and conducted twice a week per group. This structure allowed us to assess whether individuals maintained, increased, or decreased their interest and efficiency over time.

Sessions were carried out in the tunnels connecting the sleeping quarters with the outdoor enclosure, a setting that ensured optimal visibility of the individuals, reduced interference from external stimuli, and provided a naturalistic and socially stable context. Chimpanzees were free to participate for as long and as often as they chose during each session.

To ensure comparability across sessions, several control conditions were established: absence of human presence during testing, consistent use of the same type and amount of reward (fruit purée), constant availability of tools (10 rigid and 10 flexible per session), and a fixed session duration.

4.2. Procedure

The experimental sessions were conducted over an approximate period of two and a half months during April, May and June of 2025. Each group completed a total of 15 sessions (30 in total), each lasting 30 minutes and scheduled at a frequency of approximately two per week.

The devices were always placed by the responsible caretakers at Fundació Mona, who were also in charge of removing them at the end of each session. Device cleaning and disinfection, as well as tool preparation and replacement, followed the centre's internal protocols to ensure animal welfare and prevent any potential risks.

Sessions were usually held in the morning, avoiding overlap with external visitors and after the chimpanzees had explored the outdoor enclosure during their first release of the day. This timing reduced interference from external stimuli and ensured that individuals could participate under optimal conditions. The session formally began at the moment the access door to the tunnel was opened. In practice, this sometimes meant that several minutes could elapse before the first individuals entered the device, but the session time was counted from the opening of the door.

Participation was entirely voluntary and spontaneous: all five members of each social group had simultaneous access to the tunnel for 30 minutes, with complete freedom to enter and leave as often as they wished. The position of the two devices inside the tunnel remained constant, as the mounting plates were fixed in place for the entire study.

Although human presence could not be completely eliminated, it was minimized as much as possible: sessions were scheduled to avoid coinciding with public visits, and the presence of staff or volunteers in areas adjacent to the tunnels was restricted, thereby reducing distractions or external noises. Occasional environmental sounds were not specifically controlled.

The chimpanzees' very first exposure to the experimental device was already considered a formal session, and thus no prior habituation period was implemented.

4.3. Observation and coding

Chimpanzee behaviour was recorded through a continuous focal sampling system (Altman, 1974) based on video recordings of all experimental sessions. Although sessions were observed live to verify the correct functioning of the devices and ensure the safety of the individuals, the detailed analysis was carried out from subsequent viewing of the recordings. This procedure allowed for exhaustive coding of all interactions with the devices and ensured dataset replicability.

The basic unit of analysis was the bout, defined as the first action into a sequence of interactions of an individual with the experimental device. Each bout began when the chimpanzee made manual, oral, or tool contact with the experimental tube or the mounting plate and ended either when the individual initiated a new or different action, when more than five seconds elapsed without interaction, or when the individual switched to another hole, device, or tool. Bouts were coded individually, although complementary data were also collected regarding the presence of other chimpanzees in the tunnel, registered as secondary subjects.

Coding was carried out at the level of the focal individual. Each session was therefore viewed repeatedly to record the behaviour of each of the five group members. This ensured a predominantly individual-based analysis, while also documenting collective interactions such as tool transfers or competition for access to the device. The temporal resolution of all observations was expressed in minutes and seconds within the video, allowing for precise tracking of the progression of each action.

A specific ethogram (see **Table 2**) was developed for the study. An attempt was coded as successful when the flexible tool reached the end of the tube and extracted food, whereas it was coded as a failure when the tool, rigid or flexible, was withdrawn without a reward. Additional behaviours were also coded, such as partial feeding events (*sample*), defined as licking or sucking the tool or finger with potential food remains, and inspections, consisting of manual, oral, or tool exploration of the plate or the device without insertion.

Interactions were classified according to the type of contact (manual, oral, or tool-based), which were mutually exclusive categories: whenever an individual changed the

form of interaction, a new episode automatically began. Technical behaviours directed at tool modification were also recorded, with three main subcategories: *chew* (chewing the tool end), *break* (breaking the tool), and *bend* (bending it). Two modalities of combined tool use were also distinguished: *tool set*, referring to the simultaneous transport of two tools without sequential application, and *tool sequence*, defined as the sequential and optimal use of two tools to solve the task. Tool transfers between individuals were coded following the criteria established by Musgrave et al. (2020).

Data were organized in Excel spreadsheets, with each row corresponding to an episode and each column to a behavioural variable of the ethogram. Episodes were identified by session number, social group, date, and hole used. Only segments in which the camera stopped recording due to technical issues were excluded, and no incongruent data were detected. To ensure reliability, a single coder analysed all sessions twice independently, thus allowing verification of the internal consistency of the dataset.

Finally, all recordings were stored in three independent backups and labelled with the same code used in the data sheets (e.g., *S13BI01_9_06*). The only difference in the coding of video files was the addition of an extra number (1, 2, or 3) to indicate the corresponding fragment, since the camera automatically divided each session into three consecutive files. This system ensured direct correspondence between each record and its original video, facilitating the review of any episode if necessary.

4.4. Data analysis

All statistical analyses were carried out in R (version 4.4.3; R Core Team, 2025). We began with descriptive analyses to quantify chimpanzees' engagement with the task across sessions. For each individual and session, we calculated the absolute and mean counts of dips (successful and unsuccessful), inspections, and tool modifications, as well as the type of tool used (rigid vs. flexible). These descriptive summaries provided an overview of inter-individual variability and allowed visualisation of general tendencies, such as the progressive increase in flexible tool use across sessions. In addition, Pearson's product–moment correlations were performed using the cor.test function to assess associations between key performance measures, particularly between the number of dips and the number of successful dips per session.

To examine predictors of task performance, we fitted a series of generalised linear mixed models (GLMMs) with binomial error distribution and logit link function. GLMMs were selected as they are appropriate for binary outcomes, repeated observations within individuals, and multiple hierarchical sources of variation. In all models, chimpanzee identity was included as a random effect to account for repeated measures, and hole identity was included when relevant. Models were fitted using the Laplace approximation via the glmer function in the lme4 package (Bates et al., 2012). The relative contribution of fixed predictors was evaluated with Z-tests and likelihood ratio tests (LRTs; Bates et al., 2012). Multicollinearity was assessed using the vif function (Lavery et al., 2019), with all values < 2, indicating that collinearity was not a concern and that model assumptions were met.

The first model examined whether a dip resulted in food acquisition (DIP: 1 = success, 0 = failure). Fixed predictors included session number and within-session minute (to test for learning across and within sessions), sex and age (to control for demographic effects), tool modification, tool transport, tool transfer, and number of observers (to test for social facilitation). The second model assessed whether individuals were more likely to sample the tool after a dip (SAMPLE: 1 = yes, 0 = no), with the same predictors as above plus dip success as a key variable. The third model investigated predictors of tool transfer (TRANSFER_TOOL: 1 = transfer, 0 = no transfer), testing whether session progression, within-session minute, tool type, dip success, and number of observers predicted the likelihood of transfer. The fourth model examined predictors of tool transport, including session, within-session minute, number of observers, sex, age, and dip outcome. Finally, the fifth model evaluated the probability of using a rigid versus flexible tool (TOOL: 1 = rigid, 0 = flexible), with the same set of predictors.

In addition to these models, chi-square tests were performed to compare the frequencies of rigid versus flexible tool use across different temporal phases of the study. This complementary analysis allowed us to detect changes in tool preference between early and late sessions.

Together, these analyses provided a comprehensive account of chimpanzees' tool use in this novel task. Descriptive and correlational analyses established a baseline of engagement and performance, the GLMMs identified both task-related and social

factors influencing tool use, and the chi-square tests complemented these results by highlighting temporal shifts in tool preference.

4.5. Ethical considerations

This study was conducted using non-invasive methods, ensuring the welfare of the chimpanzees at all times. Sessions took place in their usual and stable environment, without physical manipulation or separation of individuals, and participation was entirely spontaneous and voluntary. The experimental devices were previously inspected by the caregiving staff to guarantee safety, and internal protocols for cleaning and preparation were strictly followed.

The ethical guidelines of the Association for the Study of Animal Behaviour (ASAB, 2024) and the internal regulations of Fundació Mona were fully respected. The procedure did not involve any negative alteration of the animals' daily routine and, instead, provided additional environmental enrichment within their living context.

5. RESULTS

5.1. Description

5.1.1. General participation of individuals

The descriptive analysis of the data collected during the experimental sessions characterises the overall pattern of participation and tool use among the nine individuals in the study group. The results reveal marked differences both in the volume of interactions and in the frequency of specific technical behaviours, highlighting considerable variability in task performance.

With regard to the total volume of inspections of the experimental device (defined as any physical contact with the structure using a tool, the mouth, or the hand), 234 inspections (see **Table 3**) were recorded across the study. Of these, 71 involved the tool (see **Table 3**), 32 were oral inspections (see **Table 4**), and 131 were manual inspections (see **Table 4**). Waty (N = 91; Mean = 6.5; SD = 9.5) and Coco (N = 68; Mean = 5.7; SD = 6.9) were the individuals with the highest number of inspections. Àfrica also showed a moderate level of activity (N = 37; Mean = 2.6; SD = 2.8), while the remaining individuals carried out very few inspections (N ≤ 14 each). Coco performed the highest number of tool inspections (N = 43; Mean = 3.6; SD = 5.4). Regarding oral inspections, Waty (N = 14; Mean = 1.0; SD = 2.4), Coco (N = 10; Mean = 0.8; SD = 1.3), and Juanito (N = 5; Mean = 0.5; SD = 0.7) stood out. Finally, in manual inspections, Waty again ranked highest (N = 66; Mean = 4.7; SD = 7.9), followed by Àfrica (N = 31; Mean = 2.2; SD = 2.3).

Subject	***Total inspections***	***Mean inspections***	***SD inspections***	***Total inspections tool***	***Mean inspections tool***	***SD inspections tool***
Àfrica	37	2.64	2.84	6	0.43	0.76
Bongo	2	0.4	0.55	0	0	0
Cheeta	3	1.5	0.71	1	0.5	0.71
Coco	68	5.67	6.92	43	3.58	5.42
Juanito	8	0.8	1.55	0	0	0
Marco	10	0.83	1.19	2	0.17	0.58
Nico	14	0.93	1.16	8	0.53	0.74
Tom	1	0.25	0.5	0	0	0
Waty	91	6.5	9.5	11	0.79	0.80

Table 3. *Descriptive statistics for total inspections and tool inspections.*

Subject	*Total inspections mouth*	*Mean inspections mouth*	*SD inspections mouth*	*Total inspections manual*	*Mean inspections manual*	*SD Inspections manual*
Àfrica	0	0	0	31	2.21	2.33
Bongo	0	0	0	2	0.4	0.55
Cheeta	0	0	0	2	1	1.41
Coco	10	0.83	1.27	15	1.25	1.76
Juanito	5	0.5	0.71	3	0.3	0.95
Marco	0	0	0	8	0.67	0.78
Nico	2	0.13	0.35	4	0.27	0.46
Tom	1	0.25	0.5	0	0	0
Waty	14	1	2.42	66	4.71	7.90

Table 4. *Descriptive statistics for mouth inspections and manual inspections.*

Overall, these results indicate that inspections were concentrated in a few individuals, reflecting marked differences in curiosity and attention directed towards the experimental device.

With regard to total task interactions (N = 1,013) (see **Table 5**), Àfrica was the most active individual (N = 355; Mean = 25.4; SD = 14.4), followed by Nico (N = 235; Mean = 15.7; SD = 9.7) and Waty (N = 129; Mean = 9.2; SD = 6.5). Marco and Coco also displayed notable participation (N = 98 and N = 70, respectively), whereas the remaining individuals engaged in fewer than 65 total interactions. In contrast, Cheeta (N = 5; Mean = 2.5; SD = 2.1) and Tom (N = 7; Mean = 1.75; SD = 1.71) exhibited only minimal involvement.

In terms of manual interactions (see **Table 6**), Àfrica (N = 35; Mean = 2.5; SD = 1.8) and Waty (N = 28; Mean = 2.0; SD = 2.0) were the most active, with Marco also showing relevant values (N = 16; Mean = 1.3; SD = 1.6). The remaining individuals displayed only anecdotal manual interactions (N ≤ 8). Regarding oral interactions (see **Table 6**), the pattern was more dispersed: Nico (N = 14; Mean = 0.9; SD = 1.7), Àfrica (N = 11; Mean = 0.8; SD = 1.0), and Waty (N = 9; Mean = 0.6; SD = 0.9) were the main contributors, while the other individuals exhibited this behaviour only sporadically (N ≤ 8).

Regarding tool use (see **Table 5**), the majority of total interactions involved instruments. Àfrica (N = 309; Mean = 22.1; SD = 13.4) and Nico (N = 213; Mean = 14.2; SD = 8.3) stood out clearly, followed by Waty (N = 92; Mean = 6.6; SD = 4.8) and Marco (N = 81; Mean = 6.8; SD = 5.9). Coco (N = 67; Mean = 5.6; SD = 5.1) and Juanito (N = 51; Mean = 5.1; SD = 3.6) also contributed substantially. By contrast, Cheeta and Tom never used tools, while Bongo showed only limited engagement (N = 38; Mean = 7.6; SD = 6.6).

Subject	***Total interactions***	***Mean interactions***	***SD interactions***	***Total interactions tool***	***Mean interactions tool***	***SD interactions tool***
Àfrica	355	25.36	14.4	309	22.07	13.4
Bongo	51	10.2	8.64	38	7.6	6.58
Cheeta	5	2.5	2.12	0	0	0
Coco	70	5.83	5.01	67	5.58	5.14
Juanito	63	6.3	4.42	51	5.1	3.63
Marco	98	8.17	6.81	81	6.75	5.89
Nico	235	15.67	9.70	213	14.2	8.34
Tom	7	1.75	1.71	0	0	0
Waty	129	9.21	6.45	92	6.57	4.77

Table 5. *Descriptive statistics for total interactions and tool interactions.*

Subject	***Total interactions mouth***	***Mean interactions mouth***	***SD interactions mouth***	***Total interactions manual***	***Mean interactions manual***	***SD interactions manual***
Àfrica	11	0.79	0.97	35	2.5	1.79
Bongo	8	1.6	2.51	5	1	1.22
Cheeta	1	0.5	0.71	4	2	1.41
Coco	1	0.08	0.29	2	0.17	0.58
Juanito	7	0.7	1.06	5	0.5	0.71
Marco	1	0.08	0.29	16	1.33	1.61
Nico	14	0.93	1.71	8	0.53	1.25
Tom	1	0.25	0.5	5	1.25	1.26
Waty	9	0.64	0.93	28	2	2.04

Table 6. *Descriptive statistics for mouth interactions and manual interactions.*

Taken together, these results demonstrate that interactive behaviour and tool use were highly variable across individuals: while some, such as Àfrica and Nico, exhibited diversified and technically rich engagement, others showed little involvement or more restricted profiles.

In relation to the use of rigid tools (see **Table 7**), Nico was the individual with the highest number of events (N = 165; Mean = 11.0; SD = 8.2), followed by Waty (N = 71; Mean = 5.1; SD = 4.2) and Marco (N = 62; Mean = 5.2; SD = 4.5). Relevant values were also observed for Coco (N = 60; Mean = 5.0; SD = 4.8) and Bongo (N = 32; Mean = 6.4; SD = 4.8), although the latter's relatively high mean was largely attributable to his low frequency of participation across sessions. By contrast, Cheeta and Tom never used rigid tools, reflecting clear within-group differences.

With regard to the use of flexible tools (see **Table 7**), Àfrica stood out markedly (N = 265; Mean = 18.9; SD = 14.0), followed at a considerable distance by Juanito (N = 31; Mean = 3.1; SD = 4.0) and Nico (N = 48; Mean = 3.2; SD = 6.8). The remaining individuals exhibited very low values: Waty (N = 21; Mean = 1.5; SD = 2.4), Marco (N = 19; Mean = 1.6; SD = 2.9), Coco (N = 7; Mean = 0.6; SD = 1.5), and Bongo (N = 6; Mean = 1.2; SD = 1.8). This pattern indicates that the use of flexible tools was highly concentrated in a few individuals, most notably Àfrica.

Subject	***Total rigid tool***	***Mean rigid tool***	***SD rigid tool***	***Total flexible tool***	***Mean flexible tool***	***SD flexible tool***
Àfrica	44	3.14	2.68	265	18.93	14
Bongo	32	6.4	4.83	6	1.2	1.79
Cheeta	0	0	0	0	0	0
Coco	60	5	4.84	7	0.58	1.51
Juanito	20	2	2	31	3.1	4.04
Marco	62	5.17	4.45	19	1.58	2.91
Nico	165	11	8.22	48	3.2	6.84
Tom	0	0	0	0	0	0
Waty	71	5.07	4.23	21	1.5	2.44

Table 7. *Descriptive statistics for tool type.*

Across the study, a total of 1,011 tool insertions into the device were recorded (see **Table 8**). Àfrica was the most active individual (N = 355; Mean = 25.4; SD = 14.4), followed by Nico (N = 235; Mean = 15.7; SD = 9.7) and Waty (N = 129; Mean = 9.2; SD = 6.5). Marco (N = 98; Mean = 8.2; SD = 6.8), Coco (N = 70; Mean = 5.8; SD = 5.0), and Juanito (N = 63; Mean = 6.3; SD = 4.4) displayed intermediate levels of involvement, while Bongo (N = 50; Mean = 10.0; SD = 8.3), Cheeta (N = 5; Mean = 2.5; SD = 2.1), and Tom (N = 6; Mean = 1.5; SD = 1.7) showed considerably lower values.

Of these, 304 were successful (see **Table 8**), with Àfrica playing a clearly dominant role (N = 232; Mean = 16.6; SD = 14.0). The remaining individuals achieved only modest results, as Juanito (N = 17; Mean = 1.7; SD = 3.0), Marco (N = 16; Mean = 1.3; SD = 2.8), and Nico (N = 25; Mean = 1.7; SD = 4.4). Waty (N = 10; Mean = 0.7; SD = 2.1) also contributed occasionally. By contrast, Cheeta, Coco, and Tom did not achieve any successful insertions, and Bongo registered only four (Mean = 0.8; SD = 1.3). Regarding failed insertions (see **Table 9**), the most notable cases were Nico (N = 210; Mean = 14.0; SD = 8.9), Waty (N = 119; Mean = 8.5; SD = 6.6), Àfrica (N = 123; Mean = 8.8; SD = 5.6), and Marco (N = 82; Mean = 6.8; SD = 5.3). Coco (N = 70; Mean = 5.8; SD = 5.0) and Juanito (N = 46; Mean = 4.6; SD = 2.3) also made relevant contributions. By contrast, Bongo (N = 47; Mean = 9.4; SD = 7.7) displayed a high mean per session despite a low overall volume, while Cheeta (N = 5; Mean = 2.5; SD = 2.1) and Tom (N = 6; Mean = 1.5; SD = 1.7) remained at very marginal levels.

Subject	***Total insertions***	***Mean insertions***	***SD insertions***	***Total exit insertions***	***Mean exit insertions***	***SD exit insertions***
Àfrica	355	25.36	14.4	232	16.57	14
Bongo	50	10	8.34	4	0.8	1.3
Cheeta	5	2.5	2.12	0	0	0
Coco	70	5.83	5.01	0	0	0
Juanito	63	6.3	4.42	17	1.7	2.98
Marco	98	8.17	6.81	16	1.33	2.84
Nico	235	15.67	9.70	25	1.67	4.35
Tom	6	1.5	1.73	0	0	0
Waty	129	9.21	6.45	10	0.71	2.13

Table 8. *Descriptive statistics for total insertions and exit insertion behaviour.*

Subject	*Total failed insertions*	*Mean failed insertions*	*SD failed insertions*
Àfrica	123	8.79	5.58
Bongo	47	9.4	7.70
Cheeta	5	2.5	2.12
Coco	70	5.83	5.01
Juanito	46	4.6	2.27
Marco	82	6.83	5.34
Nico	210	14	8.85
Tom	6	1.5	1.73
Waty	119	8.5	6.57

Table 9. *Descriptive statistics for failed insertion behaviour.*

Overall, these results show that although most individuals participated in the task, only a few, particularly Àfrica, achieved systematic and sustained success in insertions.

Regarding tool modification (physical alteration prior to or during use), a total of 66 cases were recorded (see **Table 10**). The most active individuals in this respect were Nico (N = 22; Mean = 1.5; SD = 2.8) and Marco (N = 20; Mean = 1.7; SD = 2.6), followed by Waty (N = 14; Mean = 1.0; SD = 2.0). Àfrica also displayed some modifications (N = 9; Mean = 0.6; SD = 1.5), while the remaining individuals either showed very few (e.g., Coco N = 1; Mean = 0.1; SD = 0.3) or none at all (Bongo, Cheeta, Juanito, and Tom).

In relation to tool breakage (see **Table 10**), the patterns were very similar, with a total of 60 cases. Nico (N = 21; Mean = 1.4; SD = 2.7) and Marco (N = 20; Mean = 1.7; SD = 2.6) were the main contributors, while Waty (N = 9; Mean = 0.6; SD = 1.9) and Àfrica (N = 9; Mean = 0.6; SD = 1.5) also contributed to a lesser extent. The rest of the group showed only anecdotal or no instances of tool breakage.

Finally, chewing on tools was an extremely rare behaviour (see **Table 11**), with only three cases across the entire study: Waty (N = 2; Mean = 0.1; SD = 0.5) and Nico (N = 1; Mean = 0.07; SD = 0.26).

Subject	*Total tool modification*	*Mean tool modification*	*SD tool modification*	*Total break modification*	*Mean break modification*	*SD break modification*
Àfrica	9	0.64	1.5	9	0.64	1.5
Bongo	0	0	0	0	0	0
Cheeta	0	0	0	0	0	0
Coco	1	0.08	0.29	1	0.08	0.29
Juanito	0	0	0	0	0	0
Marco	20	1.67	2.64	20	1.67	2.64
Nico	22	1.47	2.77	21	1.4	2.69
Tom	0	0	0	0	0	0
Waty	14	1	2.04	9	0.64	1.86

Table 10. *Descriptive statistics for total tool modification and break modification behaviours.*

Subject	*Total chew modification*	*Mean chew modification*	*SD chew modification*
Àfrica	0	0	0
Bongo	0	0	0
Cheeta	0	0	0
Coco	0	0	0
Juanito	0	0	0
Marco	0	0	0
Nico	1	0.07	0.26
Tom	0	0	0
Waty	2	0.14	0.54

Table 11. *Descriptive statistics of chew modification behaviours.*

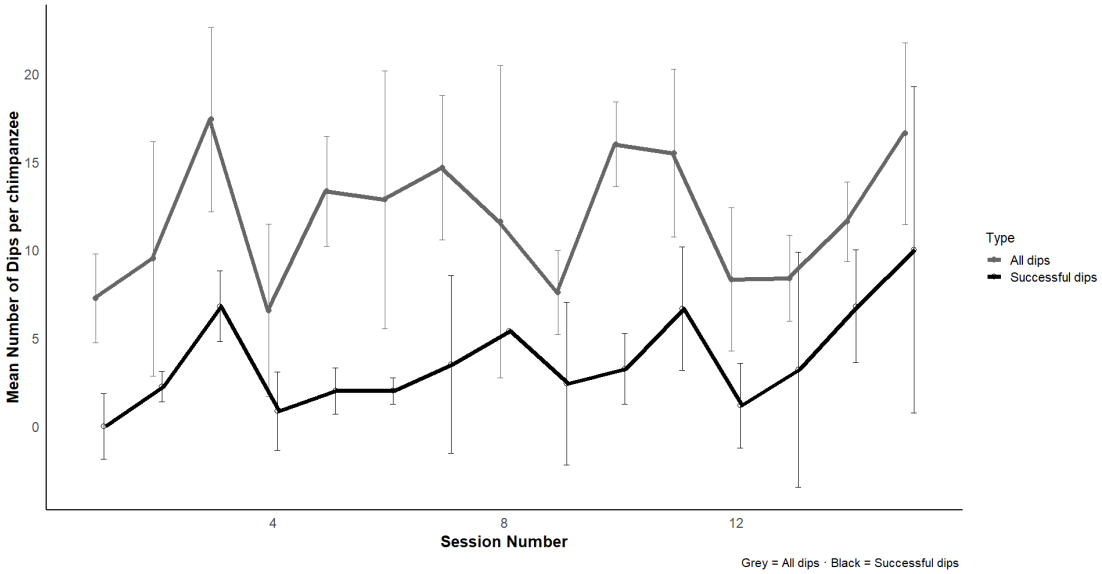
Taken together, these results highlight that while some individuals exhibited a high frequency of diverse technical behaviours, others displayed more selective profiles, focusing on specific strategies or reducing their overall level of participation. This variability may reflect differences in technical abilities, individual preferences, or levels of interest in the experimental device.

5.1.2. Task performance across sessions

Pearson's correlation analyses revealed several temporal patterns in the behaviours recorded throughout the sessions.

5.1.2.1. Insertions: overall stability and increase in success

With regard to insertions, the mean number of insertions per session remained relatively stable across the study (r(13) = .20, p = .48), with no evidence of marked temporal trends. By contrast, the number of successful insertions showed a significant positive correlation with the progression of sessions (r(13) = .55, p = .034), indicating a progressive improvement in task efficiency. Failed insertions displayed a negative but non-significant correlation (r(13) = -.30, p = .28), suggesting a possible reduction over time, although without robust statistical support.



Graphic 1. *Mean number of all and successful insertions per chimpanzee across sessions.*

5.1.2.2. Inspections: progressive reduction of exploratory behaviour

For inspection behaviours, the total number of inspections per session decreased significantly over time (r(13) = -.56, p = .031), as did manual inspections (r(13) = -.61, p = .016) and, even more markedly, oral inspections (r(13) = -.73, p = .0018). These results suggest a progressive decline in exploratory behaviour as individuals gained experience with the task. In contrast, tool inspections remained stable across the study (r(13) = .03, p = .90), showing no clear temporal trend.

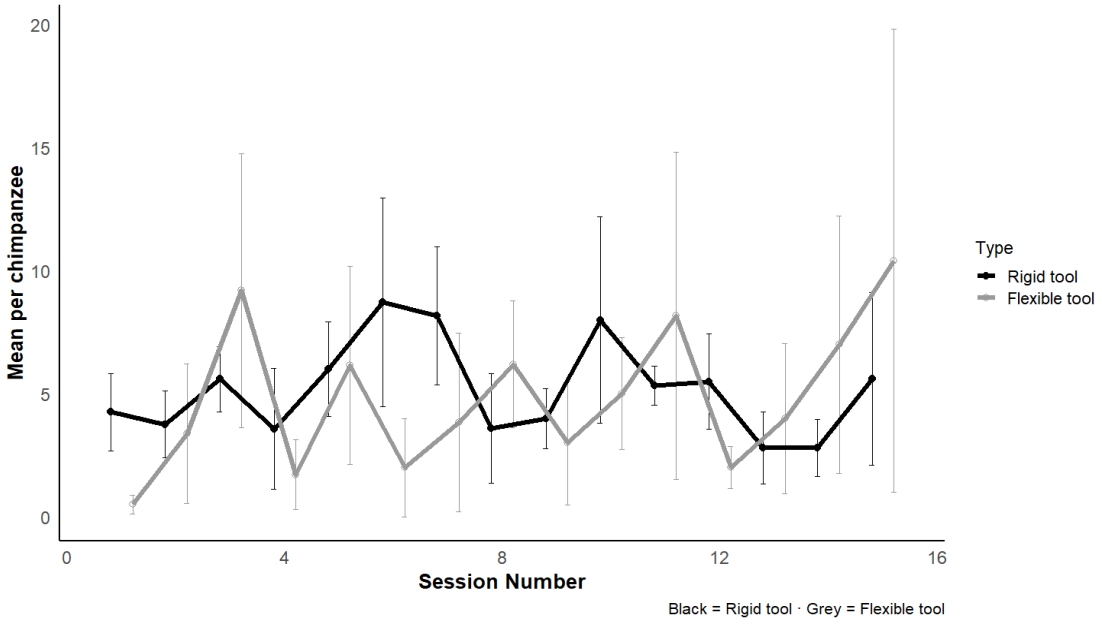
5.1.2.3. Interactions: decline in manual, stability in oral

Total interactions did not show significant changes over time (r(13) = .20, p = .48). However, manual interactions decreased significantly (r(13) = -.66, p = .007), consistent with the general reduction in manual exploratory behaviour observed in inspections.

Oral interactions remained stable (r(13) = -.01, p = .97), with no evidence of temporal variation.

5.1.2.4. Tool use: stable trends

Regarding tool use, the total number of tools used showed a positive but non-significant correlation with time (r(13) = .31, p = .27). The use of rigid tools remained stable (r(13) = -.08, p = .76), while the use of flexible tools tended to increase moderately, although without reaching significance (r(13) = .42, p = .12).



Graphic 2. *Mean number of rigid and flexible tools used per chimpanzee across sessions.*

5.1.2.5. Other technical behaviours: absence of clear trends

Tool modifications showed a slightly negative but non-significant correlation (r(13) = -.24, p = .39), while tool breakages also displayed a slight, non-significant negative trend (r(13) = -.20, p = .48). Finally, chewing on tools appeared as a sporadic behaviour without any temporal pattern (r(13) = .02, p = .97).

Overall, these results point to a general pattern of reduction in manual and oral exploratory behaviour over time, accompanied by an improvement in insertion efficiency. Other behaviours, such as the use of specific tool types or tool modifications, did not show significant variation throughout the study.

5.2. Predictive models of tool use

5.2.1. Factors predicting successful insertions

The results indicate considerable variability between individuals (var = 3.673), whereas the specific hole did not account for relevant differences (var = 0).

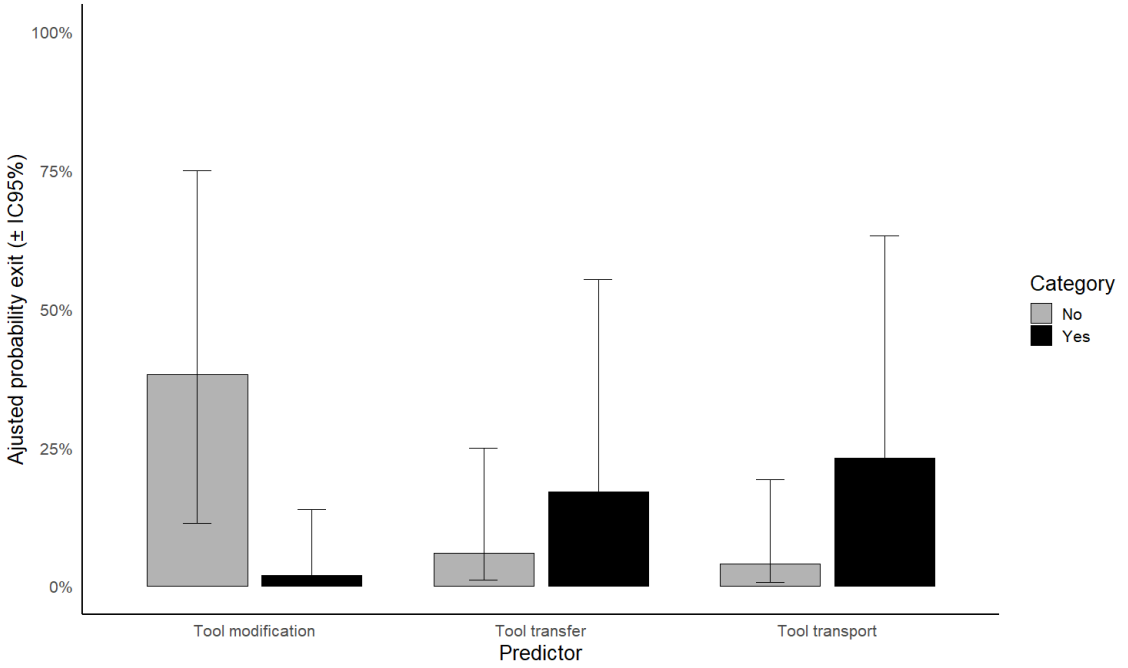
The number of cumulative sessions had a positive and highly significant effect on success (β = 1.07, SE = 0.15, z = 7.14, p < 0.001), suggesting a clear learning process throughout the study. Within each session, the probability of success also increased significantly as time progressed (β = 0.073, SE = 0.02, z = 3.79, p < 0.001), possibly reflecting adjustments in strategy or persistence in engaging with the task. With regard to technical factors, tool modification was significantly associated with a reduction in success (β = -3.39, SE = 0.72, z = -4.70, p < 0.001), while transporting a tool beforehand or receiving it from another individual clearly increased the probability of obtaining the reward (β = 1.95, SE = 0.40, z = 4.85, p < 0.001; β = 1.17, SE = 0.42, z = 2.79, p = 0.005, respectively). Individual factors such as sex (β = 0.26, SE = 1.53, z = 0.17, p = 0.864), age (β = -0.57, SE = 0.64, z = -0.90, p = 0.369), and the number of observers present (β = -0.03, SE = 0.13, z = -0.23, p = 0.819) did not show significant effects.

Overall, the model indicates that learning across sessions and specific technical behaviours, particularly tool transport and handover, were key predictors of success, whereas tool modifications tended to reduce it. The high degree of inter-individual variability suggests differences in skills or strategies employed by the chimpanzees.

Predictor	***Estimate (β)***	***SE***	***z***	***p***
(Intercept)	-2.69	1.20	-2.23	0.026
Sessions (cumulative)	1.07	0.15	7.14	< 0.001
Minutes within session	0.07	0.02	3.79	< 0.001
Tool modified	-3.39	0.72	-4.70	< 0.001
Tool transported	1.95	0.40	4.85	< 0.001
Tool received from another	1.17	0.42	2.79	0.005
Sex	0.26	1.53	0.17	0.864
Age	-0.57	0.64	-0.90	0.369
Number of observers	-0.03	0.13	-0.23	0.819

Random effects: Subject variance = 1.608; Hole variance = 0

Table 12. *Results of the GLMM (binomial distribution) assessing predictors of successful insertions.*



Graphic 3. *Adjusted probability of successful insertions depending on tool modification, transfer, and transport.*

5.2.2. Factors predicting tool transfer

The results show substantial variability between individuals in the probability of transferring a tool (var = 6.829), whereas differences attributable to the specific hole were more modest (var = 0.496).

Regarding fixed effects, the probability of tool transfer decreased significantly as sessions progressed (β = -2.62, SE = 0.50, z = –5.19, $p < 0.001$), suggesting that, over time, individuals tended to manage tools more autonomously or that the motivation to share diminished. Tool type was also a significant predictor: the use of a rigid tool significantly reduced the probability of transfer (β = -1.94, SE = 0.69, z = -2.80, p = 0.005). In this respect, individuals transferred flexible tools more frequently (Mean = 0.09; SD = 0.29) than rigid tools (Mean = 0.02; SD = 0.14), possibly due to handling difficulties or the lower shared utility of rigid implements.

The probability of tool transfer increased with time elapsed within a session (β = 0.12, SE = 0.05, z = 2.61, p = 0.009) and with a greater number of observers present (β = 0.80, SE = 0.22, z = 3.60, $p < 0.001$). Additionally, insertion outcome (success or

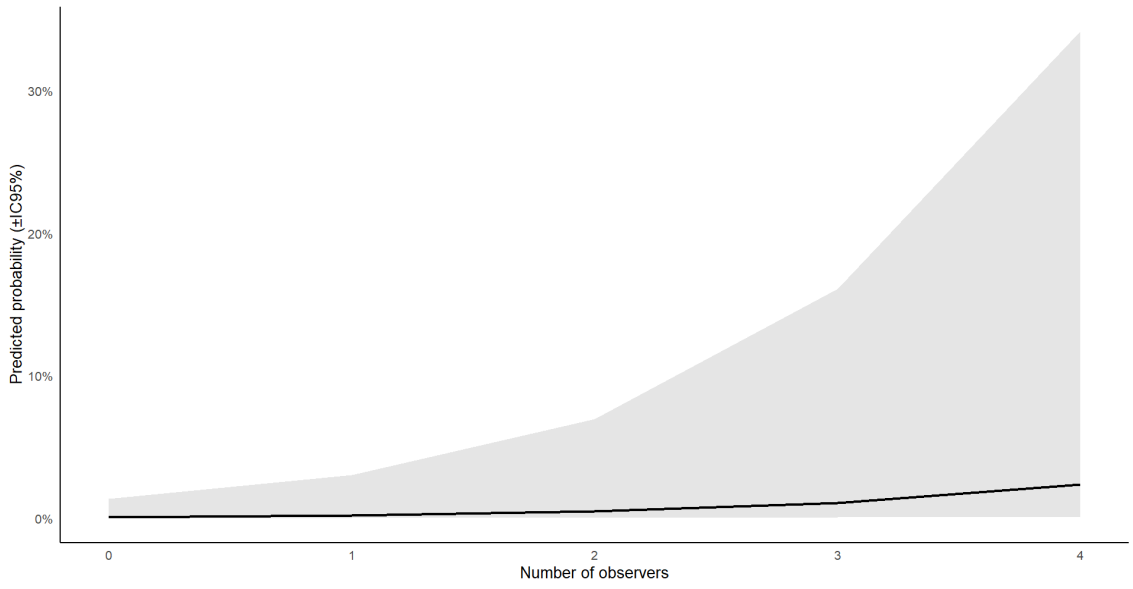
failure) marginally predicted the likelihood of tool transfer (β = 1.09, SE = 0.57, z = 1.90, p = 0.058). Individuals were more likely to transfer tools following successful insertions (Mean = 0.09; SD = 0.29) compared to failed attempts (Mean = 0.03; SD = 0.18), suggesting that transfers may be linked to recognising the effectiveness of the tool used.

In summary, these results show that tool transfer was a low-frequency behaviour, yet one that was favoured in contexts of greater social interaction and in later phases of the session, while it tended to decrease with accumulated experience and when rigid tools were used.

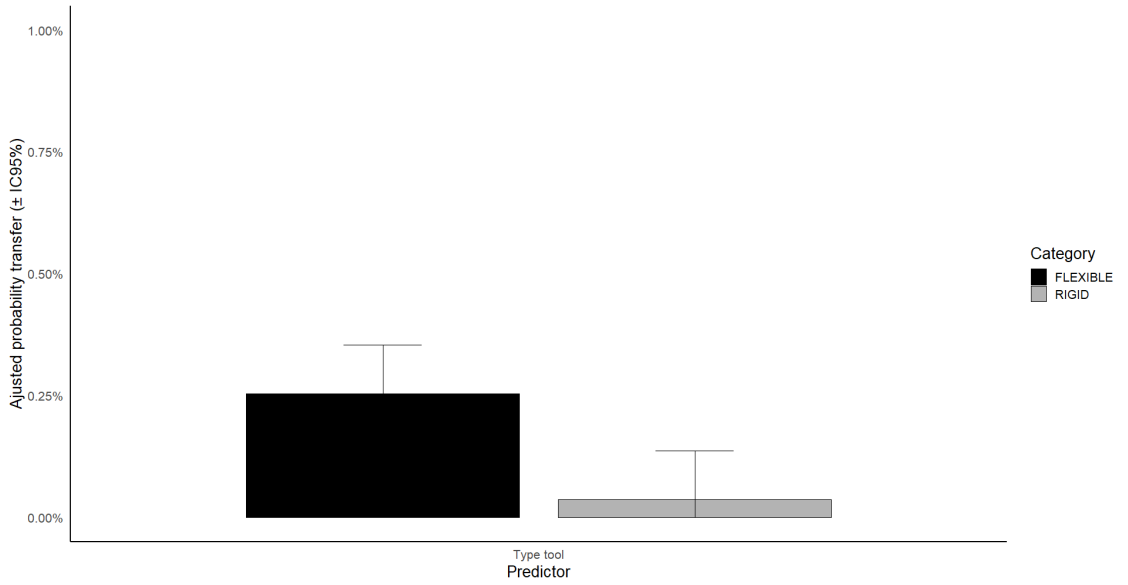
Predictor	***Estimate (β)***	***SE***	***z***	***p***
(Intercept)	-7.36	1.54	-4.78	< 0.001
Sessions (cumulative)	-2.62	0.50	-5.19	< 0.001
Minutes within session	0.12	0.05	2.61	0.009
Rigid tool used	-1.94	0.69	-2.80	0.005
Successful insertion	1.09	0.57	1.90	0.058
Number of observers	0.80	0.22	3.60	< 0.001

Random effects: Subject variance = 6.829; Hole variance = 0.496

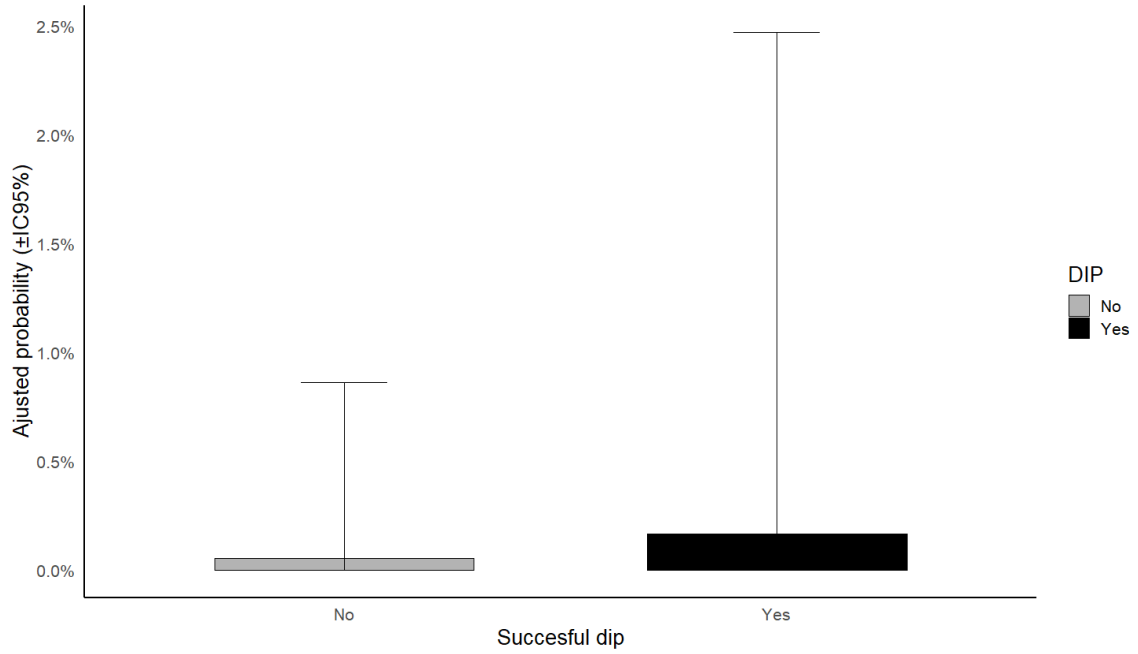
Table 13. *Results of the GLMM (binomial distribution) assessing predictors of tool transfer.*



Graphic 4. *Predicted probability of tool transfer as a function of the number of observers.*



Graphic 5. *Adjusted probability of tool transfer depending on tool type (flexible vs. rigid).*



Graphic 6. *Adjusted probability of tool transfer depending on the outcome of the preceding insertion (successful vs. failed).*

5.2.3. Factors predicting tool sampling

Inter-individual variability was moderate (var = 1.5558), while the effect attributable to the specific hole was very limited (var = 0.1771).

Among the fixed effects, the only factor with a clearly significant and strong effect was the occurrence of successful insertions, which substantially increased the probability of

sampling (β = 3.38, SE = 0.47, z = 7.21, p < 0.001). Specifically, sampling was more likely after a successful insertion [Mean = 0.96; SD = 0.19] compared to a failed one [Mean = 0.86; SD = 0.35]. A significant decrease in this behaviour was also detected as sessions progressed in time (β = -0.07, SE = 0.02, z = -3.04, p = 0.002), possibly indicating that initial exploratory actions gave way to behaviours more directly oriented towards extraction.

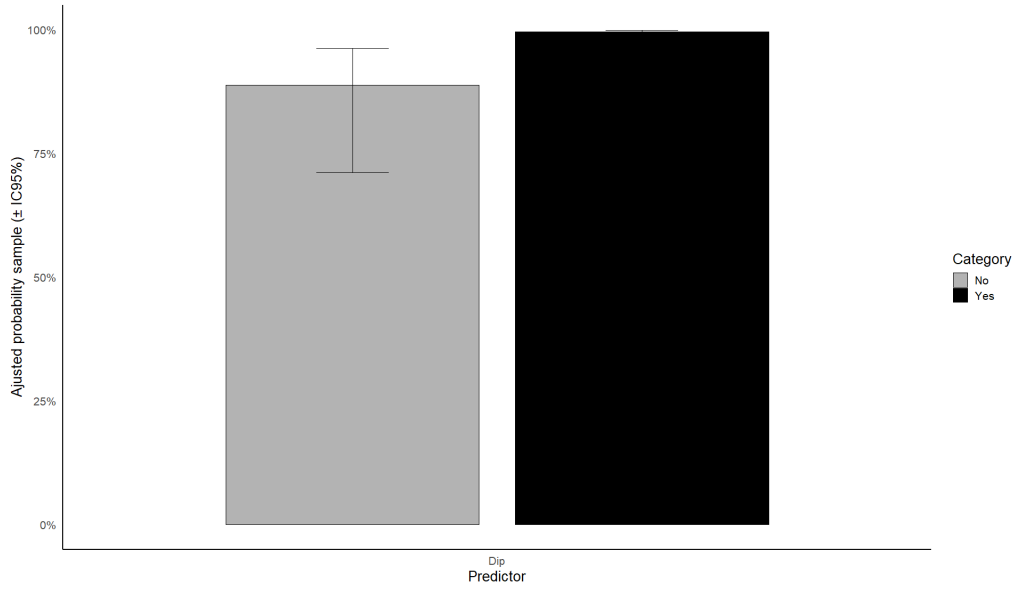
Other predictors showed non-significant trends: the number of cumulative sessions (β = 0.28, SE = 0.17, z = 1.66, p = 0.097) suggested a slight increase in sampling in later sessions, while the use of rigid tools (β = 0.56, SE = 0.35, z = 1.59, p = 0.112) might have been associated with a marginally higher frequency. In contrast, the remaining predictors (number of observers, age, and sex) did not reveal any meaningful differences, indicating that tool sampling was independent of social or demographic factors.

Overall, these results suggest that tool sampling was a relatively frequent behaviour, especially when preceded by successful insertions, but it tended to be concentrated in the earlier phases of each session. The analysis indicates that the probability of chimpanzees bringing the tool to their mouth after an insertion was mainly associated with the success of the dip, while the other predictors (tool type, number of observers, age, and sex) did not present significant differences. This suggests that sampling behaviour depended primarily on the immediate effectiveness of the preceding insertion.

Predictor	***Estimate (β)***	***SE***	***z***	***p***
(Intercept)	2.27	0.66	3.43	<0.001
Sessions (cumulative)	0.28	0.17	1.66	0.097
Minutes within session	-0.07	0.02	-3.04	0.002
Rigid tool used	0.56	0.35	1.59	0.112
Successful insertion	3.38	0.47	7.21	< 0.001
Number of observers	0.12	0.15	0.81	0.418

Random effects: Subject variance = 1.556; Hole variance = 0.177

Table 14. *Results of the GLMM (binomial distribution) assessing predictors of tool sampling*.



Graphic 7. *Adjusted probability of tool sampling depending on the outcome of the preceding insertion (successful vs. failed).*

5.2.4. Factors predicting tool transport

Inter-individual variability was moderate (var = 0.9374), while no variance was attributable to the specific hole (var = 0).

Regarding fixed effects, a clear temporal pattern emerged: as sessions progressed, the probability of transporting a tool decreased significantly (β = -2.53, SE = 0.25, z = -9.94, $p < 0.001$). This may indicate that, with accumulated experience, individuals already had tools available nearby or reduced the need to move them. A distinct social effect was also observed: a greater number of observers reduced the probability of transporting tools (β = -0.83, SE = 0.17, z = -4.90, $p < 0.001$), possibly due to competition or inhibition in the presence of conspecifics.

The remaining factors did not show statistically significant effects: tool type (β = -0.29, SE = 0.41, z = -0.73, p = 0.469), time within the session (β = -0.01, SE = 0.02, z = -0.52, p = 0.603), and previous success in obtaining the reward (β = -0.17, SE = 0.50, z = -0.35, p = 0.726) appeared not to influence the decision to transport tools.

Overall, these results suggest that tool transport was a relatively infrequent behaviour, particularly in the later stages of the study and in contexts with a high presence of other individuals.

Predictor	*Estimate (β)*	*SE*	*z*	*p*
(Intercept)	-2.96	0.58	-5.06	< 0.001
Sessions (cumulative)	-2.53	0.25	-9.94	< 0.001
Minutes within session	-0.01	0.02	-0.52	0.603
Rigid tool used	-0.29	0.41	-0.73	0.469
Successful insertion	-0.17	0.50	-0.35	0.726
Number of observers	-0.83	0.17	-4.90	< 0.001

Random effects: Subject variance = 0.937; Hole variance = 0

Table 15. *Results of the GLMM (binomial distribution) assessing predictors of tool transport*.

5.2.5. Factors predicting the choice and use of instruments

Random effects indicated considerable inter-individual variability (var = 1.608), while no variance was attributable to the specific hole (var = 0).

Regarding fixed effects, the progression of the study had a clear impact: as sessions advanced, the probability of using a rigid tool decreased significantly (β = -0.64, SE = 0.13, z = -5.08, p < 0.001). A similar temporal effect was observed within sessions, as the likelihood of employing a rigid tool was lower in later minutes (β = -0.06, SE = 0.02, z = -3.64, p < 0.001).

Previous tool transfer significantly reduced the probability of selecting a rigid tool (β = -1.01, SE = 0.44, z = -2.29, p = 0.022). In transfer contexts, individuals selected rigid tools less frequently (Mean = 0.21; SD = 0.41), relying proportionally more on flexible ones, whereas in non-transfer contexts rigid tools were chosen more often (Mean = 0.55; SD = 0.50). Likewise, when tools had been transported, the probability of selecting a rigid tool was reduced (β = -1.36, SE = 0.31, z = -4.30, p < 0.001). Conversely, prior tool modification significantly increased the likelihood that the tool was rigid (β = 2.05, SE = 0.49, z = 4.24, p < 0.001). This result suggests that individuals performed modifications more frequently on rigid tools than on flexible ones. Other

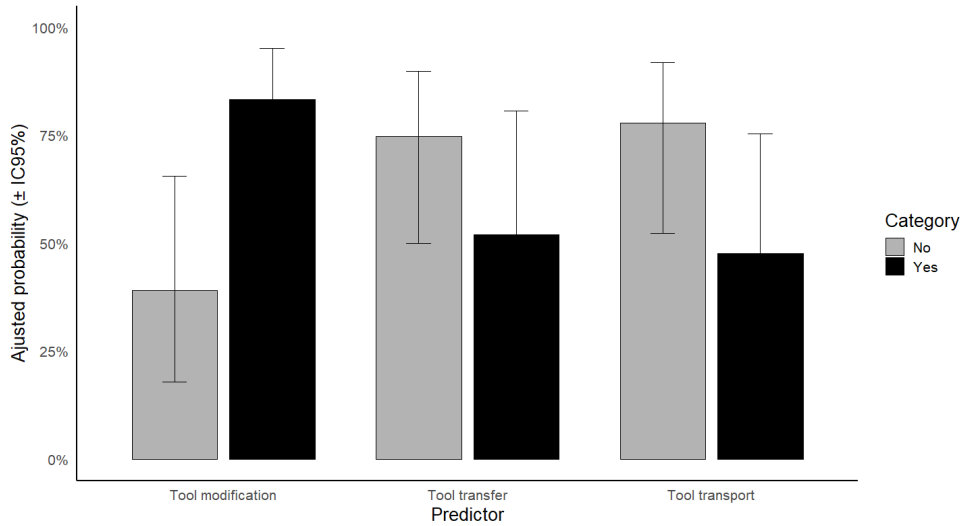
factors, such as the number of observers (β = -0.03, SE = 0.12, z = -0.26, p = 0.798), sex (β = 0.57, SE = 1.01, z = 0.57, p = 0.569), and age (β = 0.09, SE = 0.08, z = 1.16, p = 0.246), did not show statistically significant effects.

Overall, these results suggest that the choice of rigid tools was favoured by their prior modification but decreased with the progression of the sessions, in later stages within a session, and in contexts where tools had been transported or transferred by other individuals.

Predictor	*Estimate (β)*	*SE*	*z*	*p*
(Intercept)	-1.56	2.39	-0.65	0.52
Sessions (cumulative)	-0.64	0.13	-5.08	< .001
Minutes within session	-0.06	0.02	-3.64	< .001
Tool transferred	-1.01	0.44	-2.29	.022
Tool transported	-1.36	0.31	-4.30	< .001
Tool modified	2.05	0.49	4.24	< .001
Number of observers	-0.03	0.12	-0.26	.798
Sex	0.57	1.01	0.57	.569
Age	0.09	0.08	1.16	.246

Random effects: Subject variance = 1.608; Hole variance = 0

Table 16. *Results of the GLMM (binomial distribution) assessing predictors of rigid vs. flexible tool choice.*



Graphic 8. *Adjusted probability of selecting a rigid tool depending on tool modification, transfer, and transport.*

5.2.5.1. Sequential use of tools

Although chimpanzees eventually stabilized the task and achieved success, the specific step involving the use of the flexible tool was not systematically understood. Subjects did not consistently follow the expected sequence of first employing the rigid tool and then immediately switching to the flexible one. Only two individuals (Àfrica and Bongo) showed clear instances of such sequential use, after which they persisted with their own preferred strategies. These events were rare and mostly descriptive, but they highlight that chimpanzees only partially grasped the overall task structure.

To complement this qualitative observation, chi-square analyses were conducted to assess whether tool selection reflected an understanding of the task's structure. At the global level, individuals employed rigid tools more frequently than flexible ones (Rigid = 441, Flexible = 384; $\chi^2 = 3.94$, df = 1, $p = 0.047$). However, temporal dynamics revealed a shift: in the first ten sessions, rigid tools were chosen significantly more often than flexible tools (Rigid = 352, Flexible = 265; $\chi^2 = 12.27$, df = 1, $p < 0.001$), whereas in the last five sessions the pattern reversed, with flexible tools being selected significantly more frequently (Flexible = 168, Rigid = 121; $\chi^2 = 7.64$, df = 1, $p = 0.0057$). This pattern confirms the tendency observed in correlation analyses across sessions: although not statistically significant, a consistent decrease in the use of rigid tools and a corresponding increase in the use of flexible tools was detected. These results suggest that, as the study progressed, chimpanzees became increasingly likely to use the flexible tool, indicating that they gradually understood at least part of the task structure, though not the entire sequence.

6. DISCUSSION

6.1. Interpretation of the Present Results

From this study, we obtained results that allow us to address our main objectives. The experiment was designed to evaluate chimpanzees' spontaneous engagement with a novel tool-use task that required the execution of a sequence of actions. Accordingly, the analyses considered both technical aspects, such as success in food extraction, exploration patterns, and tool-related behaviours including transport and modification, and the potential influence of social and demographic traits such as age, sex, group membership, number of observers, and tool transfer. Within this framework, our findings revealed a high degree of variability across individuals, both in terms of participation, the types of tools used (rigid vs. flexible), the ways in which they were employed, and the extent to which the task was successfully completed. Although the experimental device was available to the entire group, fewer than half of the individuals engaged with it in a meaningful way. Most group members displayed either a passive attitude, very brief or sporadic involvement, or even a complete lack of participation, as in the case of Víctor. This pattern is consistent with a broad body of literature emphasising individual variability as a constant trait within primate groups (Boesch & Boesch, 1990; Whiten et al., 1999). Such variability has been interpreted as a key factor for understanding differences in learning capacities, motivation, participation, and even the emergence of differentiated technical strategies within groups.

In the experimental context of this study, these individual differences may have been accentuated by the absence of real ecological pressures and the artificial nature of the task, which may have been perceived as irrelevant by some individuals. Recent work has suggested that factors such as personality, age, group hierarchy, or previous life history can decisively shape the predisposition to engage in technical tasks (Gruber et al., 2015). In our case, the lack of participation by several individuals may be related to advanced age or complex life histories, as previously noted in similar contexts by Lonsdorf (2006) and Hopper et al. (2015a). It is important to underline that the absence of active participation does not necessarily indicate a complete lack of attention or interest; rather, it may reflect an alternative way of interacting with the experimental stimulus.

Task success was concentrated almost exclusively in a single individual, Àfrica, who exhibited a high number of successful insertions, consistent participation across sessions, and a clear preference for flexible tools. Moreover, in the final sessions she developed an innovative technical variant: she used the rigid part of the flexible instrument to perforate the paper barrier and subsequently employed the more pliable end to extract the reward. This behaviour demonstrated a notable capacity for exploration and cognitive flexibility. Such an unequal distribution of success has also been reported in other studies, often interpreted as the result of one or more "expert models" within the group (Boesch & Boesch, 1990; Hopper et al., 2015b). In this case, however, no clear evidence of behavioural transmission to other individuals was observed, despite the continuous presence of this competent model. This absence of diffusion is not unusual in experimental contexts and has been documented previously as a consequence of limited motivation to imitate, the inherently individual nature of certain innovations, or the artificial character of the task (Clay & Tennie, 2018; Kendal et al., 2018). Another relevant aspect is the individual's position within the group hierarchy. Interestingly, Àfrica was not the most dominant member of the group, which suggests that factors beyond social rank, such as tolerance, experience, or individual disposition, may have been decisive in shaping her engagement and technical success. Furthermore, these findings reinforce the idea that the presence of a competent model is not, in itself, a sufficient condition to generate social learning, particularly in the absence of additional facilitating factors such as prior familiarity with similar tasks, shared interest, or social cohesion between the model and potential observers (Gruber et al., 2019).

Within the subgroup that did engage, distinct technical strategies were detected. While Nico relied almost exclusively on rigid tools, Àfrica consistently used flexible instruments, and Marco was responsible for the few observed episodes of tool modification. These differences may reflect a degree of individual specialisation, which is consistent with previous studies documenting considerable variability in the types and uses of tools among chimpanzees (Sanz et al., 2009; Yamamoto et al., 2013). In Marco's case, the modification of a tool's extremity may indicate some capacity for technical innovation, although the limited number of observations precludes robust conclusions. Nevertheless, such actions could represent early forms of spontaneous

technical behaviour that, in other contexts, might be transmitted and consolidated culturally.

Regarding the evolution of behaviour across sessions, some individuals appeared to improve with practice, whereas others lost interest after initial unsuccessful attempts. This pattern could reflect a degree of individual learning through trial and error, but it may also point to a limited causal understanding of the relationship between the tool, the device, and the reward. In many cases, repeated attempts were observed with unsuitable tools, or explorations took place outside the device, suggesting an exploratory rather than a structured planning approach. According to Povinelli (2000), chimpanzees often act through association rather than a deep causal understanding, and their instrumental behaviour can be highly sensitive to contextual and perceptual cues. In this regard, Bandini & Tennie (2017) argue that many apparently complex behaviours may emerge independently, as latent solutions within the species, rather than through faithful transmission between individuals.

Taken together, these observations suggest several implications. On the one hand, the individual capacity to solve technical tasks is evident, particularly in the case of Àfrica, yet this capacity did not translate into observable behavioural diffusion within the group. On the other hand, the combination of concentrated success, diverse strategies, and limited individual progress suggests that, although the group had the material and social conditions for social learning, this did not occur in a detectable way. Subtle forms of observation or learning may have taken place, but their impact on final behaviour was, at best, limited. These findings are consistent with other studies that have questioned the actual frequency of social transmission among chimpanzees in controlled experimental settings (Clay & Tennie, 2018).

In sum, the present results highlight a high degree of behavioural variability, both in terms of participation and in the strategies and success achieved, with one individual standing out in particular. No clear processes of social transmission were observed, and most successful behaviours appear to be the result of individual innovation or personal experimentation. This body of evidence provides the basis for a deeper analysis of the underlying mechanisms and sets the stage for comparison with the existing literature.

6.2. Design and Context-Related Factors

The analysis of the results obtained from this task cannot be separated from the specific conditions under which the study was conducted. Both the experimental design and the captive context in which the individuals were situated may have decisively influenced the behaviours observed, as well as their transmission, or lack thereof. This section explores the main contextual and methodological elements that may have shaped the findings.

First, it is important to note that the study was carried out at Fundació Mona, a rescue centre, rather than in a wild environment or a strictly controlled research setting such as a laboratory. This entails many ecological limitations but also offers certain advantages. On the one hand, the captive context provides a unique opportunity to observe each chimpanzee's behaviour in relation to the experimental task under relatively stable conditions, with regulated access to the stimulus and continuous audiovisual recording that allows for detailed analysis. Such an environment facilitates the establishment of repeatable experimental conditions and makes it possible to control certain external variables that, in natural contexts, would be practically impossible to isolate.

Nevertheless, the same environment also presents significant limitations. The study group does not represent a naturally formed social community, but rather a collection of individuals rescued from diverse backgrounds, such as former circus animals, pets, or ex-zoo inhabitants. This diversity of origins implies considerable heterogeneity in previous experiences, levels of socialisation, learned technical skills, and relationships with humans (Lonsdorf, 2006; Hopper et al., 2015a). Some individuals may have had greater exposure to manipulable objects or to human interactions that facilitated certain forms of individual learning, while others may have experienced greater difficulties in adapting to problem-solving contexts.

In addition, the social dynamics within the group may not faithfully reflect those of wild communities. Although hierarchies and affiliative relationships were established, the backgrounds of some individuals and the absence of kinship ties could have negatively influenced group cohesion, social attentiveness, and willingness to observe or copy others' behaviours. This is especially relevant considering that social transmission requires not only the presence of an innovator or expert model, but also a social

structure that supports opportunities for attention, interaction, and the maintenance of traditions (Whiten, 2011; Gruber et al., 2019). In this case, although Àfrica potentially fulfilled the role of a model, the lack of interest or attentiveness from the other chimpanzees may have prevented any observable transmission.

Regarding the design of the experimental apparatus, several limitations should also be noted, as they may have affected the success of attempts and, particularly, the level of causal understanding. One of the most significant aspects concerned the limited availability of causal information provided by the apparatus. When inserting the rigid tool, individuals could not clearly see the internal barrier of the tube, nor whether it had been pierced, due to the opacity of the first 12 cm. This lack of visual feedback may have constrained trial-and-error learning and reduced the association between action and outcome. Similar effects have been described in other studies using opaque devices or mechanisms with low transparency, which tend to lower the probability of success (Horner & Whiten, 2005; Povinelli, 2000). In natural contexts, by contrast, chimpanzees perforate termite mounds themselves with a rigid tool, directly observing the causal link between the action of piercing and the visible result of a new hole (Sanz & Morgan, 2007). In our study, the pre-established and unchanging insertion points, together with the opacity of the device, may therefore have obscured the necessity of sequential tool use and reduced the extent to which environmental scaffolding channelled individuals towards the correct order of actions.

Moreover, the fact that the task required a sequence of two actions using two different tools (one rigid and one flexible), in a specific order, in order to reach the goal, increased its technical complexity. Such cognitive demands involve motor planning, inhibition of immediate responses, and the capacity to recall the correct sequence, skills that have been associated with advanced forms of instrumental manipulation (Stout et al., 2008; Bandini & Tennie, 2017). The difficulty of the task may have discouraged participation from less persistent individuals or those with limited previous experience in technical problem-solving, thus contributing to the low overall participation observed. It is also possible that the required sequence was not intuitive for most of the group, favouring only the more exploratory or persistent individuals.

Another factor to consider is temporal. Although this study involved a greater number of sessions compared to other similar works (Bernstein-Kurtycz et al., 2020), the number of sessions was still insufficient to allow robust conclusions to be drawn. Social learning and the acquisition and diffusion of innovative behaviours rarely occur immediately; rather, they require repeated exposure to the task, direct observation of successful actions, and time to consolidate such new behaviours (Whiten, 2021). In this study, most individuals had few attempts and limited opportunities to observe successful interactions directly. It is possible that with more sessions, some indication of transmission might have emerged, particularly among younger or more exploratory individuals.

Finally, it is necessary to reflect on the influence of the artificial context on the manifestation of technical behaviour. Although chimpanzees are capable of solving experimental tasks, they are often situated outside their natural ecological environment, which can profoundly affect their motivation and comprehension. Boesch (2012) has argued that artificial contexts, no matter how controlled, may provide only a partial picture of primates' cognitive repertoires, and that natural conditions are essential for understanding animal culture in its full complexity. This does not invalidate studies conducted in captivity, but it does call for their results to be interpreted with caution and regarded as only one part of the broader body of available evidence.

In conclusion, both the captive context and the specific design of the apparatus may have significantly influenced the results obtained. The absence of observed transmission should not be interpreted as definitive evidence for the non-existence of culture in chimpanzees, but rather as an illustration of the constraints imposed by certain contexts and experimental designs. These considerations are fundamental for assessing the extent to which the results may be generalised, and for critically evaluating the potential of captive studies to inform our understanding of the evolution of technical culture in hominins.

6.3. Comparison with Previous Studies and Theoretical Debates

The results of this study are situated within a longstanding yet still unresolved debate concerning the existence, nature, and limits of culture in chimpanzees. Since the late

twentieth century, increasing evidence has suggested that chimpanzees exhibit behavioural variability across groups, tool use in diverse contexts, and a degree of social transmission (Whiten et al., 1999; Boesch & Boesch, 1990). This diversity has been interpreted as evidence of non-human cultural traditions, socially transmitted but not reaching the levels of complexity or cumulative character typical of human culture.

The patterns observed in the present study highlight, on the one hand, the importance of individual variability as a key factor for understanding chimpanzee technical behaviour. Such variability has been documented in both wild and captive contexts, manifesting in tool choice, strategies of use, and success rates (Boesch, 2012; Whiten, 2017a). The fact that only a subset of individuals engaged actively, and that success was concentrated in a single group member, does not contradict existing models, but rather nuances them: it demonstrates that culture, if present, is not evenly distributed within the group, and that transmission is neither automatic nor universal.

Nevertheless, the case examined here shows a marked absence of observable behavioural transmission, even in the presence of a competent and persistent individual such as Àfrica. This finding resonates with the position advanced by Tennie, Call, and Tomasello (2009), known as the “latent solutions” hypothesis. According to this perspective, many behaviours observed in chimpanzees do not in fact spread through social learning, but instead emerge repeatedly through individual innovation within a shared cognitive and ecological framework. Tennie et al. (2020) reinforce this view, showing that in experimental contexts chimpanzees tend to act exploratively but do not adopt novel behaviours observed in others unless there is strong prior understanding or highly explicit reinforcement.

It is important to note, however, that within cognitive ethology there is no consensus on what precisely constitutes social transmission, nor on which mechanisms are required to classify a behaviour as culturally transmitted. Whiten (2011) proposes a graded continuum, ranging from social facilitation and local/stimulus enhancement to emulation and imitation, each associated with different levels of cognitive complexity and fidelity. By contrast, Tennie et al. (2020) argue that only high-fidelity forms of copying, such as imitation proper, could explain cumulative culture. From this

perspective, passive observation or the use of the same tool without exact replication of another's action would not suffice as evidence of cultural transmission.

The results of this study indicate that, despite the sustained presence of a competent model (Àfrica), no other group member adopted her strategy or showed signs of attempting to replicate it. This could reflect the absence of imitation or emulation processes, or a lack of social attention and interest in the task. Such a pattern is not unusual: multiple studies have documented cases where the presence of an expert does not necessarily lead to behavioural diffusion (Clay & Tennie, 2018; Kendal et al., 2018). Similarly, Vale et al. (2020) found that chimpanzees with access to social information did not outperform controls in technical tasks, while Watson et al. (2017) showed that novel behaviours introduced by subordinates often failed to spread within the group. Even in wild populations, innovations may remain restricted to a single individual for years, without transmission, reinforcing the idea that chimpanzee culture is more fragile and partial than that of humans.

At the same time, the tool transfers observed in our study may be understood as a complementary form of cooperation that provides potential scaffolding for individual learning. Although most evidence on tool transfers as teaching comes from wild populations, particularly at Goualougo (Musgrave et al., 2016; 2020), the fact that captive chimpanzees in our study engaged in consistent exchanges of tools indicates a notable degree of within-group tolerance. While such behaviour does not constitute full cultural transmission, it highlights prosocial tendencies that may represent precursors to more complex forms of cooperation and social learning.

By contrast, other researchers have argued that chimpanzees are capable of maintaining stable traditions over time, sometimes with considerable fidelity. For instance, Luncz and Boesch (2014) documented marked differences in tool use between neighbouring groups in the same region, despite comparable access to resources, suggesting active and enduring cultural transmission. Furthermore, authors such as Whiten (2011, 2017a, 2021) and Boesch (2012) have proposed that chimpanzees may be best understood as occupying an intermediate position within a "cultural continuum," situated between the predominantly individual innovation seen in other species and the cumulative culture characteristic of humans.

This concept of a cultural continuum is particularly useful for interpreting the present findings. On the one hand, it moves beyond the classic dichotomy of "culture present" versus "culture absent," recognising the possibility of intermediate levels of transmission and complexity. On the other hand, it frames chimpanzees as a species possessing technical and social capacities that point towards nascent forms of culture, while remaining far from the so-called "ratchet effect" that characterises human culture. This effect, as described by Whiten (2017a), involves not only transmission but also the progressive accumulation of improvements across generations, something not yet clearly documented in great apes.

In this sense, the present results seem to occupy a middle ground: they reinforce Tennie et al.'s (2020) position concerning the absence of high-fidelity transmission in experimental contexts, but at the same time, Àfrica's competence and persistence could have served as a model under different conditions. The lack of observed transmission may therefore not reflect a general incapacity among chimpanzees, but rather the specific circumstances of this study: the limited number of sessions, the scarcity of direct social interactions during the task, or the low motivation of other individuals to observe and learn.

It should also be acknowledged that cultural transmission is likely influenced by multiple variables: the degree of group cohesion, the nature of the behaviour to be transmitted, the length of exposure, and the degree of transparency of the task (Whiten, 2021; Gruber et al., 2019). Thus, the absence of transmission in this study does not necessarily imply that the group was incapable of developing it, but that the conditions required for such processes did not materialise.

Finally, the notion of a continuum is not only useful for interspecies comparisons, but also for reflecting on the evolutionary processes that gave rise to cumulative culture in humans. The ability to modify tools, select appropriate materials, experiment with new strategies, and, in some cases, transmit them, constitutes an essential set of precursors for cultural evolution. Studying these capacities in chimpanzees therefore provides a valuable comparative model. The findings presented here, despite their limitations, contribute to this comparative framework and help to situate chimpanzees within the

broader evolutionary landscape of culture, as a species positioned midway between solitary innovation and cumulative transmission.

6.4. Connection with Archaeology and Human Evolution

The results obtained in this study provide relevant insights into the debate on the evolutionary origins of human material culture. Although chimpanzees do not possess a cumulative culture comparable to that of humans, their technical behaviours, individual variability, and capacity to manipulate tools offer valuable clues for understanding the conditions that may have favoured the emergence of complex material culture in early hominins.

One of the most notable aspects of the present study is the requirement for the sequential and differential use of two tools to solve the task, as well as the occasional modification of tools. Such behaviours involve motor planning, inhibition of immediate responses, and the ability to associate different actions in a functional sequence, all of which are considered key elements in the emergence of lithic technology (Stout et al., 2008; Stout, 2011).

These observations are consistent with neuroarchaeological studies that have linked planned tool use with specific activations in the prefrontal cortex, a brain region implicated in complex decision-making and working memory (Stout & Hecht, 2017; Stout et al., 2018). The presence of some of these capacities in chimpanzees suggests that the cognitive foundations necessary for the manufacture and complex use of tools may have been present, in embryonic form, in the last common ancestor of humans and great apes (Hopkins et al., 2017), and that subsequent evolution likely consisted of the expansion and progressive integration of these capacities (Smaers et al., 2017).

Another relevant element is the marked individual variability observed within the group. While most individuals showed little interest or technical skill, a reduced number demonstrated clear competencies, and one individual clearly stood out as a technically efficient model. This pattern is consistent with the idea that technological innovations may initially have been introduced and maintained by particular individuals, occupying a central role within the group, as suggested by Haslam (2014) and Wynn & Coolidge

(2010) in relation to early hominins. This reinforces the hypothesis that material culture did not emerge as a homogeneously distributed capacity within the group, but rather as a specialised activity that was only gradually shared as more efficient mechanisms of transmission developed.

Although no clear behavioural transmission was observed in this study, the presence of complex technical behaviours, persistence in the task, and adaptive capacity in some individuals represent significant indicators of evolutionary potential towards more sophisticated forms of culture. Several authors have argued that cumulative culture was not a sudden invention, but rather the result of a series of pre-existing capacities that combined and reinforced one another (Whiten, 2017; Migliano & Vinicius, 2021). A similar gradualist view has been advanced in primate archaeology, where percussive behaviours are considered a cross-species foundation for the emergence of lithic technology (Harmand & Arroyo, 2023). These capacities include the ability to manipulate diverse materials, strategic flexibility, innovation, and, above all, the possibility of sharing knowledge within the group.

From this perspective, the present study contributes valuable data to the comparative model in palaeoanthropology: chimpanzees are capable of displaying forms of technical behaviour that, while not cumulative or clearly transmitted, share functional structures with the earliest lithic industries. Laland & Janik (2006) already suggested that primate data could serve as a reference for defining the minimum threshold of capacities necessary for the emergence of material culture, and subsequent studies have reinforced the value of this comparative approach for interpreting the earliest archaeological record (Braun et al., 2025; de la Torre & Hirata, 2015; Luncz et al., 2024; Pascual-Garrido, 2024).

This connection between primatology and archaeology is especially pertinent when considering the notion of a cultural continuum: chimpanzees, although lacking cumulative culture, are situated within an evolutionary process in which culture does not appear suddenly but is gradually built upon existing capacities. The fact that such capacities can be observed in partial form in chimpanzees supports the idea that early hominins may have developed technology gradually, as favourable social, ecological,

and cognitive conditions for transmission and accumulation of knowledge were established.

Finally, it should be stressed that studies in captivity have the potential to provide systematic and detailed data on behaviours that are difficult to observe in natural contexts or to reconstruct from material remains. While such studies must be interpreted with caution, they can offer reference models for the interpretation of the archaeological record, particularly regarding action sequences, real-time decision-making, and the diversity of technical strategies within a single group. In this sense, the results obtained here contribute to linking two disciplines often treated separately, primatology and archaeology, through a shared evolutionary perspective.

7. CONCLUSIONS

The aim of this dissertation has been to evaluate how chimpanzees (*Pan troglodytes*) approach a novel instrumental task requiring the sequential use of tools, and to analyse which individual and social factors modulate success, participation, and technical performance. This approach has been framed from a comparative perspective, with the goal of contributing to the understanding of cultural transmission processes in primates and to the debate on the origins of human material culture. The combination of an innovative task, systematic behavioural recording, and statistical analysis of both social and technical variables has provided an integrated view of the mechanisms involved in learning and tool use in primates.

The results show that participation, success, and technical performance were not evenly distributed within the groups but were concentrated in a reduced subset of individuals. These individuals were often characterised by greater prior technical experience or by high levels of social tolerance, suggesting that both individual background and group dynamics play a decisive role in the acquisition of technical skills. A preference for flexible tools was also observed, together with consistent patterns of transfer between group members, indicating that socialisation processes directly influenced instrumental practice and learning. These observations are consistent with previous studies highlighting the importance of social interactions in the diffusion of technical behaviours, and they reinforce the idea that primate culture is a collective phenomenon rather than a purely individual one. Predictive analyses further confirmed that variables such as age, sex, number of observers, and repeated exposure significantly influenced the probability of success, and the strategies employed.

Overall, these findings demonstrate that tool use in chimpanzees cannot be explained solely as the outcome of individual abilities, but rather as the result of a complex interaction between technical, social, and contextual factors. The study also highlights the value of controlled captivity: despite its limitations in terms of ecological validity, such environments enable systematic assessment of technical and social dimensions and provide information that is difficult to obtain under natural conditions.

Some limitations must, however, be acknowledged. The reduced sample size and number of sessions restrict the generalisation of the results, and the captive context, despite its naturalistic design, differs inevitably from the ecological conditions of wild habitats. For this reason, the results must be interpreted with caution and understood primarily as an exploratory approach that opens new avenues for research.

Despite these constraints, the contributions of the study are clear. It emphasises that chimpanzee technical behaviour arises from an interaction between social and individual factors, and it offers a comparative framework linking primatology, archaeology, and palaeoanthropology. Taken together, the results support the idea that the antecedents of human material culture did not appear abruptly but are rooted in gradual processes already present in other primates. This perspective reinforces the view of culture as a continuous evolutionary process, rather than as an exclusive and emergent human trait.

Thus, this dissertation contributes to the understanding of culture as a shared evolutionary phenomenon, showing that the study of chimpanzee technical behaviour can provide new keys to understanding the foundations of our own cultural evolution. Ultimately, the research presented here is intended as a starting point for future studies that may further explore the role of innovation, transmission, and social variability in the cultural processes of primates.

8. FUTURE PERSPECTIVES

A particularly relevant line of research would be to develop a second experimental phase aimed at overcoming the limitations identified in this study while simultaneously deepening the social dimension of learning. This proposal would involve ensuring that at least one group member acquired prior competence in solving the sequential task. To achieve this, it would be possible to work in a guided manner with the collaboration of the responsible caregiver, who could act as a model to help a selected individual achieve a full understanding of the instrumental sequence. This initial step would provide a solid basis from which to explore how the rest of the group members may learn by observing a competent individual within their own social environment.

Once this individual mastered the task, the experiment could be replicated under conditions similar to the present study but with the presence of a competent model within the group. Such a design would not only facilitate the assessment of direct observation but would also make it possible to analyse how factors such as hierarchy, social tolerance, or prior familiarity between individuals interact when imitating or adopting new strategies. It would also be particularly relevant to examine whether tool transfers emerge in this context, as such behaviours have been interpreted in the literature as possible incipient forms of teaching and cooperation.

Beyond enabling a more refined analysis of the processes of social learning, this second phase would provide valuable information on the possibility that the behaviour might become stabilised at the group level—that is, ceasing to be a punctual occurrence and instead becoming a pattern shared within the community. This scenario would represent an important advance in understanding the conditions required for certain technical innovations to evolve from individual explorations into part of a collective repertoire with cultural value.

This study can also serve as a starting point for new lines of research within cognitive archaeology, a discipline that seeks to integrate evidence from primatology, neuroscience, and archaeology to understand the origins of material culture. One especially promising avenue lies in establishing more direct connections between the

patterns observed in other primates and the key questions surrounding the earliest lithic industries.

In particular, it is crucial to investigate how processes such as individual innovation, social transmission, and the potential collective stabilisation of an instrumental behaviour can provide a comparative model for analysing the emergence and consolidation of the first stone technologies. This approach would make it possible to link the experimental study of instrumental behaviour with the earliest archaeological record, offering new tools for interpreting the transition from individual explorations to shared practices with cultural value.

In this way, the combination of primate research and archaeological analysis opens new perspectives on the gradual emergence of human material culture, reinforcing the idea of an evolutionary continuum between other primates and the earliest hominins.

In conclusion, this study highlights that the investigation of sequential tool use in chimpanzees represents a research field with high potential for further development. Both the implementation of new experimental phases in naturalistic captivity and the connection with the earliest archaeological record underscore the importance of continuing to advance along this line. Still in full development, cognitive archaeology must systematically integrate evidence from non-human primates in order to progress towards a deeper understanding of the gradual processes that gave rise to human material culture.

9. LISTS

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