



# Animal culture in non-human primates: a review

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## ABSTRACT

In the last decades, a large number of cultural behaviours have been reported across different taxa. The main evidence is found in non-human primates. Nevertheless, even though its existence is broadly accepted in the scientific field, there is controversy regarding the nuances to define animal culture, its extent and if this type of culture is equal to the human one.

In this bibliographic review, we analysed a total of 60 studies, following a modified version of the PRISMA 2020 declaration. We delve into the criteria defining culture and its interplay with genetics, ecology and behavioural evolution. We categorized for social learning and transmission the paths -vertical and horizontal-, mechanisms -such as social enhancement, response facilitation and imitation- and biases -such as sex, rank, prestige or bond-. In addition, we approach to the influence of tolerance or innovative and conformist behaviours; discuss about the factors explaining the stability of traditions; and present the most relevant statistical methods in animal culture research.

This field of science has only just started to be studied. However, we can begin to glimpse the parallels between human culture and that of other primates, as well as the complex processes explaining the presence of animal culture in non-human primates.

**Keywords:** Animal culture, behaviour, primates, social learning, traditions





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## 1. INTRODUCTION

The presence of culture in animals is becoming more widely accepted in the scientific community. However, animal culture being in the spotlight has caused serious questions about whether it is an exclusively human trait (Perry, 2009). Nevertheless, ongoing debate persists about whether the behavioural diversity found in both animals and humans, constituting culture, can be considered of the same type. Thus, there is controversy regarding the nuances to define animal culture and its extent (Nakamura & Nishida, 2013). Yet, when genetic and environmental factors fail to explain variations for the same behaviour between groups of the same species, the presence of specific knowledge or skills could be explained through animal culture (van Schaik & Pradhan, 2003). In contrast, some authors propose that such behavioural traits might be explained by a complex interplay between the genetic, the environmental and the cultural factor itself (Nakamura & Nishida, 2013).

In recent decades the number of animal behaviours reported and classified as cultural has been growing. These cultural repertoires encompass behaviours across a diverse range of species, from mammals -such as monkeys, great apes and cetaceans- to birds, fish and even insects (Hobaiter & Byrne, 2010).

The main evidence supporting the existence of traditions in animal behaviour comes from studies on bird songs and the specialization in foraging techniques observed in primates, including tool-using conducts (see Figure 1) (Laland & Janik, 2006; Hobaiter & Byrne, 2010). Diverse cultural behaviours are observed, such as the dialects in bird songs or the way British tits open milk bottles. In primates, examples include the meticulous washing of potatoes in Japanese macaques, the strategic fishing for termites, the use of some leaves as antiparasitic, or employing various techniques to crack nuts in chimpanzees. Even experiments with guppies have evidenced their ability to socially learn new routes or ways of foraging (Voelkl & Noë, 2008).





**Figure 1:** An example of chimpanzees using sticks as tools (Miller Greg, 2005).

The ways in which new skills are acquired through social learning are diverse, ranging from independent learning, such as social enhancement, to observation and copying of peers, such as imitation (Laland & Janik, 2006). Moreover, animals also engage in acts of innovation or conformism, when relying on their traditions (Lehner *et al.*, 2010; Péter *et al.*, 2022). Nevertheless, the intricate question persists: How do socially learned behaviours diffuse within and between populations, giving rise to the emergence of culture? This phenomenon, decisive for the stability of traditions within a population, remains incompletely explained (Claidière & Sperber, 2010; Watson *et al.*, 2017).

Hence, it is crucial to consider a non-anthropocentric perspective when determining whether a behaviour is considered cultural or not in non-human animals. This holistic approach would help to understand the evolution of behaviour in different taxa and the emergence of animal traditions (Laland & Janik, 2006).

Each day we learn more about the cognitive abilities of chimpanzees, bonobos, gorillas and orangutans, noting how their capacities are similar to those of a two or three year-old human child (Casal Paula & Singer Peter, 2022). It is well-known that chimpanzees are our closest relatives genetically speaking, sharing almost 99% of our DNA. In fact, chimpanzees are more closely related to humans than to gorillas. Nevertheless, it remains surprising that they exhibit behavioural patterns so closely resembling to ours. These living beings are capable of feeling emotional and physical





suffering, and have complex capacities such as imagination (Cavalieri Paola & Peter Singer, 1993). Nonetheless, the question of whether these non-human species deserve rights comparable to humans is still an ongoing debate (Casal Paula & Singer Peter, 2022). We, as humans, have an obligation not only to protect, conserve and ensure the well-being of these brother species, but also to remove the blindfold obscuring that humans, in the end, are just another hominid (Cavalieri Paola & Peter Singer, 1993). Consequently, the content of this review is relevant to the investigation of cognitive evolution and culture in humans and is therefore of importance in the anthropological and psychological study of our species. Acquiring knowledge and studying these animals provides us a broader insight into the behavioural similarities across species and raises awareness of current global issues such as wildlife poaching or deforestation, emphasising the importance of environmental conservation (Casal Paula & Singer Peter, 2022).

Therefore, the aim of this bibliographic review is to break down some of the walls that prevent us from seeing the behavioural, social and cultural proximity we share with the rest of the primates and animals, as well as to research on a debate that is still a matter of controversy to this day.





## 2. OBJECTIVES

- To conduct a systematic review of the animal culture in non-human primates.
- To assess the criteria determining whether specific animal behaviours can be qualified or not as cultural.
- To discuss whether culture represents a distinctive human trait or a shared characteristic among other animals.
- To investigate the intricate interplay between culture, genetics, ecology and behavioural evolution.
- To categorize the mechanisms for social learning, transmission and innovation of cultural behaviours in animals.
- To illustrate the behavioural parallels between humans and non-human primates within a cultural context.
- To present the most relevant statistical methods in animal culture research.





### 3. METHODOLOGY

This bibliographic review approaches the PRISMA 2020 declaration, which follows a series of 27 items to ensure the transparency of bibliographic reviews through methodical steps (Page *et al.*, 2021). However, a modified PRISMA 2020 declaration was used, adapting the original one (meant for meta-analysis) to this review.

The selection of articles for this review was carried out in March 2023 and was extracted from PubMed and Science Direct databases. For this purpose, articles from the last 20 years were selected. The filter used for the search was:

“((((((animal culture) NOT (birds)) NOT (insects)) NOT (humans)) AND (behaviour)) AND (social learning)) AND (primates)”.

Thus, we obtained articles matching our criteria containing the keywords “Animal culture”, “Behaviour”, “Social learning” and “Primates”, avoiding those including “Birds”, “Insects” and “Humans” as keywords. The criteria was chosen on the basis of the diagrams and concepts network proposed by Viciano (2021). Hence, “Animal culture”, “Behaviour”, “Social learning” and “Primates” were terms highly cited among scientific literature about animal behaviour research (Viciano, 2021). However, some articles did not meet the criteria established and were therefore discarded from this review. A total of 92 articles were displayed after the search with these filters. Thus, 63 results were shown in PubMed, while 29 results were shown in ScienceDirect. On the one hand, from those 63 articles from PubMed, 1 was excluded because it was in Russian language, 4 were discarded because they were not accessible, and 2 were excluded because they did not fit the topic of this bibliographic review. On the other hand, from those 29 articles from ScienceDirect, 2 were excluded because they were not accessible, 1 was discarded because it was duplicated and 24 were excluded because they did not fit the topic of the review either. Thus, we extracted from the databases 56 publications from PubMed and 3 from ScienceDirect, making a total of 58 articles and a total of 33 publications excluded from the results.

In addition, two publications and one book out of the filter were added in order to give background and expand on some of the concepts covered in this review: (Whiten *et al.*, 2001), (Whitehead *et al.*, 2019) and (Cavalieri Paola & Peter Singer,

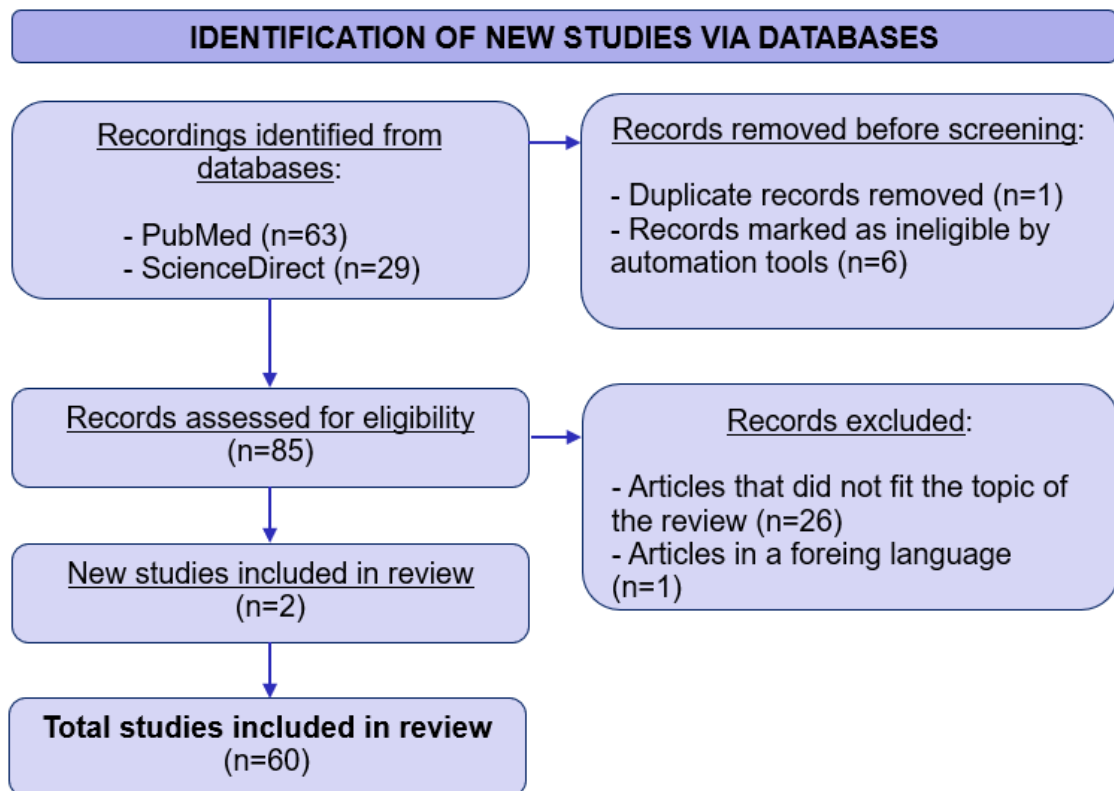






1993). On the one hand, both of these articles were highly cited in various publications of the bibliographic review and they contributed to give cohesion to this project. On the other hand, the book has great importance in topics such as the cultural transmission in primates.

Therefore, the total amount of articles for this review is 60 (see Figure 2).



**Figure 2:** PRISMA 2020 modified flow diagram template for systematic reviews (Page *et al.*, 2021).



## 4. RESULTS AND DISCUSSION

### 4.1. Animal culture:

A significant debate has unfolded over the last few decades concerning the definition of animal culture and its comparability to the culture observed in humans (Nakamura & Nishida, 2013). This ongoing discourse persists within the scientific community. We will address this debate on the broad definitions for this controversial term and the premises proposed by some authors, highlighting key considerations in defining and classifying animal culture and social learning.

In general terms, the broadest accepted definition of animal culture includes the learned behaviours present in a group of individuals that are maintained and transmitted fully or partially through social learning (Jaeggi *et al.*, 2010; Lehner *et al.*, 2010; Lamon *et al.*, 2017). Some authors extend this definition emphasizing that these cultural traits must endure through generations, as a way of another kind of inheritance besides the genetic one (Samuni *et al.*, 2020). Nevertheless, others defend it should include the innovation of behaviours contributing to the emergence of new cultural behaviours within a population of individuals (van Schaik & Pradhan, 2003). In contrast, Perry (2009) points out that social learning involves variations in an individual's behaviour repertoire influenced by: actively observing another individual's behaviour; the passive accompanying of another individual while performing a task; or the interaction with the remainings from activities that might lead to the discover of the behaviour. Thus, it includes either observation or interaction with an individual of the group or its products (Hoppitt & Laland, 2011). Expanding on this, social learning also defines how individuals prefer to display a behavioural variant adopted by the majority of the group rather than their own -based on the individual's prior knowledge of how to solve the same task-, even when there is no apparent advantage (Huffman *et al.*, 2010). This concept was illustrated, among others, through the research of van Leeuwen *et al.* (2014) and their discovery of the so-called “grass-in-ear behaviour”, where chimpanzees inserted a stick of grass in one ear, demonstrating the capacity of these animals to copy behaviours without any adaptative value (see Figure 3).





**Figure 3:** Grass-in-ear behaviour in the group: **a.** Julie (the inventor); **b.** and **c.** other group members copying the behaviour (*red arrows*) (van Leeuwen *et al.*, 2014).

Some authors declare that the stronger the social influence is, the more it will take to homogenise the behavioural differences between groups, meaning populations with their own behavioural variants will take longer to reach homogeneity if each group has a significant reason to keep its variant (Claidière & Sperber, 2010). These dynamics can be defined by three factors: the first states that social influence is greater when a larger number of individuals exhibit the same behaviour; the second suggests that social influence is lower when individuals have more time to explore new alternatives independently; and the third, the social influence will be lower the greater the proportion of naïve individuals in the group (Claidière & Sperber, 2010).

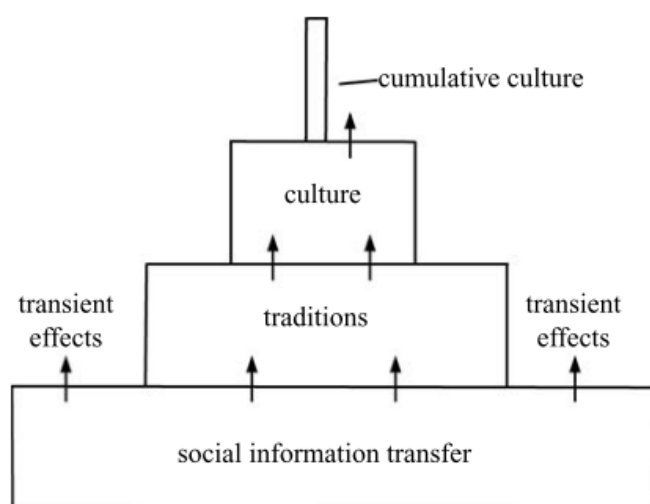
In addition, the debate on animal culture also revolves around the difficulty of demonstrating how much of a behaviour is influenced by social learning mechanisms. Although social learning has been extensively demonstrated in captive-bred animals, it is much more complex to do so with those present in the wild (Gruber *et al.*, 2012).

van Schaik Carel P. *et al.* (2003) propose that the difference in culture between populations is due to the complexity of innovative behaviours, as well as the mechanisms for social learning. Therefore, they identify four cultural elements that help to explain the appearance of new behaviours based on their complexity: (i) labels: referring to processes that require little innovation, such as the identification of food or



predators; (ii) signals: such as sounds; (iii) skills: with tool-use behaviour as the most notorious example; (IV): symbols: conforming signal variants specific of a population. Among the non-human primates, only chimpanzees and orangutans have been demonstrated to present the first three cultural elements. However, chimpanzees seem to have a larger and more diverse repertoire compared to orangutans, possibly due to their gregarious nature (Whiten & van Schaik, 2007). Meanwhile, humans can perform all of these elements (van Schaik Carel P. *et al.*, 2003). Thus, human symbolic skills and their complexity represent the main difference from the rest of the primates (van Schaik Carel P. *et al.*, 2003).

Whiten & van Schaik (2007) conceptualize social learning as a pyramid built up in four different layers (see Figure 4). The base is formed by the transmission of social information present across different taxa. The upper stratum consists of traditions based on the social knowledge found in the base. The third layer involves the set of traits and variations of these traditions, giving rise to culture. Finally, the last level of the pyramid leads to the presence of cumulative culture evolution, shaping a stratified and intertwined culture. This last layer is the principal explanation for the sophistication observed in human culture.



**Figure 4:** Social learning pyramid (Whiten & van Schaik, 2007).

In order to be able to classify a behaviour as cultural or not when it comes to research, Whiten & van Schaik (2007) propose three aspects that must be taken into account: (i) the environmental and genetic factors that could explain the behaviour under study must be excluded; (ii) recordings of subjects of different ages in





observation processes must be available; (iii) a series of premises based on past studies through controlled experiments must be reachable.

As previously discussed, it is essential to contemplate the correlation between genes and animal traditions and their reciprocal influences. Consequently, we might wonder how culture affects genetics. It is no surprise that individuals migrating to new communities not only introduce a genetic pool but also bring along their cultural repertoires (Whiten A., 2007). Moreover, it is to be expected that a trait will disappear if a more beneficial one is introduced, eventually leading to homogenisation within the group (Perry, 2009). From this relationship comes the term gene-culture evolution, "occurring when cultural evolution shapes genetic evolution, often but not always entailing reciprocal interactions between the two" (Whitehead *et al.*, 2019, p. 2). In this case, social learning helps to reduce genotypic differences between individuals through the erosion of phenotypic differences. The theory suggests that human adaptability to the environment without major genetic changes could be explained through this mechanism (Whitehead *et al.*, 2019).

Other theories, such as the Baldwin Effect, aim to demonstrate the close relationship where phenotypic plasticity and changing environmental conditions act as a selection filter beyond the genetic factors. This theory tries to explain how some organisms can adapt rapidly to an environment where genetic changes do not occur fast enough (Corbey, 2020). Consequently, this interplay plays a pivotal role in comprehending the evolution of behaviour (Samuni *et al.*, 2020).

In cases where the line between genetics, environment, and culture is so thin, various hypotheses can be formulated for the same behaviour. For instance, consider the comparison of nettle-feeding techniques between captive and wild gorillas. A hypothesis put forward by Byrne *et al.* (2011) proposed a cultural explanation for this behaviour, refuting an earlier theory leaned towards a genetic interpretation. On the contrary, Shelly Masi (2011) suggested a third hypothesis centred on the bioavailability of certain plants in the gorillas' environment. Thus, it proposes that the ingestion of specific plants may be due not to genetic or cultural factors, but could be linked to the nutritional deficit in fibre of some of the gorillas in captivity.





Another example could be the list of behaviours classified as cultural in chimpanzees, drawn up by Whiten *et al.* (2001). Through the method of exclusion, they initially ruled out genetic and environmental influences for the occurrence and distribution of certain behaviours. However, some of these traits are found to be influenced by these two elements. A representative case is the use of different sticks in size in chimpanzees to collect ants, attributed to different cultural variants. Later on, it was confirmed that they selected a different size of stick depending on the aggressiveness of the ant species -thus, being influenced by the environment-. Therefore, a plausible conclusion is that cultural repertoires can be explained to different extents through a combination of genetics, culture, and environment (Nakamura & Nishida, 2013). Nonetheless, Gruber *et al.* (2009) claim to have experimentally demonstrated the first evidence of animal culture controlling for the environmental element. It compares two populations of the same chimpanzee subspecies in Uganda that have been shown to be genetically indistinguishable. This research investigated the difference in honey extraction techniques from holes present in a horizontal log, conducted in two populations of chimpanzees (see Figure 5).



**Figure 5:** a. Chimpanzee observed while feeding (Carey & Hagstrom, 2009); b. Sticks manufactured by chimpanzees during honey acquisition (Gruber *et al.*, 2009).

In any case, it would be essential to carry out experimental intervention in the studies; otherwise, it becomes challenging to rule out hypotheses based on genetic or environmental factors. Nevertheless, organizing such experiments poses hurdles for science not only in terms of logistics but also in the ethical considerations and welfare of the animals involved (Whiten A., 2007). In addition, research focusing on animal



behaviour has to try to find quantitative methods to differentiate social learning in both natural and captivity groups (Hoppitt & Laland, 2011).

#### **4.2. Cognitive evolution in primates:**

Social learning plays a crucial role in the selection of specific genetic variations. Thus, we may wonder how the development of animal culture is correlated with the increased cognition and encephalisation processes (Whitehead *et al.*, 2019).

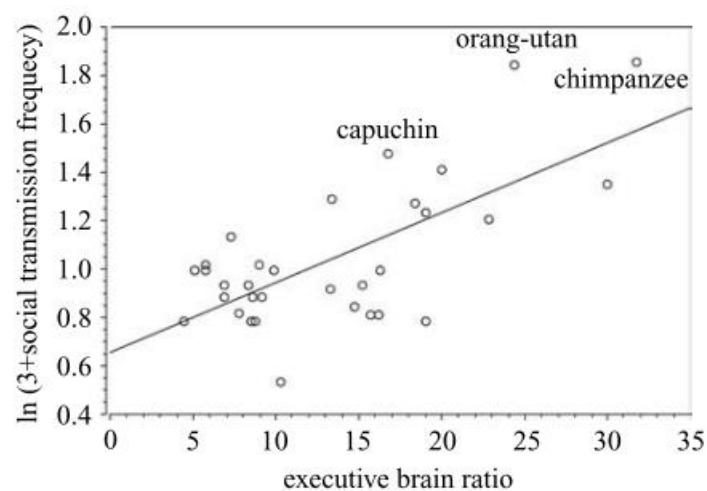
The cultural intelligence hypothesis mentions that the acquisition of social skills during the developmental phase enhances an individual's intellectual capacities (Whiten & van Schaik, 2007; Forss *et al.*, 2016). In this work-line, we find acquired specialisations, defined as behaviours whose development is independent of genetic or environmental factors. Instead, these behaviours are cultivated by individuals through either independent innovation or specific social learning mechanisms (van Schaik & Pradhan, 2003). Moreover, it is expected that the evolution of enhanced intelligence, leading to the establishment of traditions, is more likely to happen in gregarious species, such as chimpanzees or capuchin monkeys, among other species. In fact, chimpanzees present a greater encephalization than orangutans. In such species, acquired specializations might endure through socially based learning, suggesting a social origin for increased intelligence in primates (van Schaik & Pradhan, 2003). Forss *et al.* (2016) demonstrated for the first time the veracity of the cultural intelligence hypothesis in a non-human species, stating that the recurrence of social learning has led to evolutionary and consequential cognitive differences between two orangutan species. Thus, in captive conditions under homogeneous environmental settings provided by zoos, Sumatran and Bornean orangutans were introduced to different tasks to test their problem-solving abilities. In context, in the wild, Sumatran orangutans exhibit greater tolerance and more opportunities for social learning -due to a broader gregarious nature- compared to Bornean orangutans. However, orangutans are considered solitary species in contrast with other primates. Consequently, Sumatran orangutans have a more extensive cultural repertoire than their Bornean counterparts (Forss *et al.*, 2016). The results of this research were clear: Sumatran orangutans performed better in the different cognitive tests in comparison to Bornean





orangutans, being in concordance with predictions of the cultural intelligence hypothesis (Forss *et al.*, 2016).

Concerning the link between the frequency of social learning and encephalization in different primates, its direct correlation has been statistically confirmed in some papers (see Figure 6) (Whiten & van Schaik, 2007). Notably, regardless of encephalization, capuchin monkeys, orangutans and chimpanzees exhibited the highest frequency of socially acquired learning. However, culture is not only defined by all those traits that are transmitted through social learning; it also involves behavioural innovations of asocial origin that contribute fluidity to traditions (Whitehead *et al.*, 2019). These findings collectively challenge previous propositions that suggest that social learning plays a more crucial role in the development of brain size than asocial learning. Thus, the interplay between these two learning types mutually sustains culture and nurtures cognitive intelligence in these species (Whiten & van Schaik, 2007). Furthermore, this dynamic interaction helps elucidate the mechanisms through which innovations spread among individuals, eventually becoming a group tradition (van Schaik & Pradhan, 2003; Whitehead *et al.*, 2019).



**Figure 6:** Frequency of social learning is plotted against executive brain ratio (Whiten & van Schaik, 2007).

Moreover, Furlong *et al.* (2008) claim to have empirically demonstrated for the first time variations in the development of tool-use skills depending on the degree of enculturation in captive chimpanzees. Enculturation, in this context, refers to the need for a human caregiver to actively promote social and communicative interactions for a







young chimpanzee raised in captivity (Furlong *et al.*, 2008). Thus, this study revealed that enculturated chimpanzees correlated more easily the use of a tool with a subsequent reward. They also displayed higher alertness, cooperation, relaxation, confidence, and coordination compared to non-reared chimpanzees. In summary, enculturated chimpanzees exhibited a higher rate of success in tasks including tool-using performance and those requiring paying attention to others (Furlong *et al.*, 2008).

Another perspective, linked to long-term memory, has been proposed to assess the development of intelligence and retrospective abilities in problem-solving challenges. Vale Gill L. *et al.* (2016) presented the first evidence of long-term memory in chimpanzees showing that most individuals could solve a task proposed almost four years after initial exposure by relying on long-term memory. Meanwhile, similar results were obtained in other studies examining fidelity and memory in marmoset monkeys (Gunhold *et al.*, 2015). This is evidence of the capacity for retrospective memory in these animals to solve future problems and emphasizes the role of memory in sustaining traditions over time. Furthermore, the combination of long-term memory and the capacity for innovation transmitted through social learning allows the sedimentation and accumulation of traits, leading to the formation of a complex culture (Gunhold *et al.*, 2015; Vale Gill L. *et al.*, 2016).

These evidences enable us to understand how some species have successfully colonized new niches and habitats without the need for profound genetic changes, illustrating how cognitive evolution helps to maintain animal traditions (Whiten & van Schaik, 2007).

#### **4.3. Innovations and conformity:**

Understanding the cognitive mechanisms that facilitate the transmission of traditions becomes particularly relevant as we explore the characterization of innovations. Lehner *et al.* (2010, p. 4) define innovation as “a behaviour shown in some populations or individuals, but not in others, where its absence is due to a lack of knowledge rather than different physical or social conditions or different genetic backgrounds”. The spread of an innovative behaviour involves its observation by another individual, creating a chain with subsequent observers. However, not all new





traits become disseminated in a population. For this to occur, they must possess the intra-group fidelity required to evolve into a tradition (Dindo *et al.*, 2011; Gunhold *et al.*, 2015). Furthermore, Lehner *et al.* (2010) affirmed that a behaviour can be considered an innovation if it satisfies three criteria: first, it must not be displayed by all specimens. Second, it must not be performed in a particular state of the individual -such as infanticide by males after conquering a group-. Third, to distinguish an innovation from an accidental behaviour it must be exhibited at least twice.

With reference to the emergence of innovations, the innovation-and-diffusion hypothesis proposes that innovations typically originate from individuals who introduce part of their cultural repertoire to a group with different traditions. In addition, it suggests that the local cultural repertoire of a population results from the origin and extinction of specific behaviours -due to the failure of social transmission, among other factors-. Finally, it emphasizes that the habitat functions as a funnel where behavioural variants converge in a relatively predictable way (van Schaik Carel P. *et al.*, 2003). A clear representation of innovative individuals is found in those who migrate to other subpopulations. In chimpanzees, it is often the females that leave the group upon reaching adulthood. It thus symbolizes not only an opportunity to spread genes but also traditions in a new social context (Lycett *et al.*, 2010). Péter *et al.* (2022) suggest that the well-digging behaviour observed in an East African chimpanzee population was imported by an immigrant female. This evidenced that the immigration of individuals offers new avenues for innovation within the groups they join. Another possibility for the origin of innovations, in the absence of migrant specimens, is the presence of juveniles in the group. These individuals tend to be less conservative in food selection and investigate more than their adult counterparts (Biro *et al.*, 2003). However, the success rate in the spreading is lower when originating from a juvenile (Tan *et al.*, 2018).

Focusing on primates in the wild and captivity, we find some distinctions in innovations, observing that animals in captivity tend to exhibit a broader range of innovative behaviours. Even some animals reintroduced into the wild continued to show a greater innovative repertoire compared to wild populations. It is believed that this should be explained by the absence of dangers in the habitat of animals in captivity. Such animals, when presented with a new stimulus, may associate it with





food rewards or positive reinforcement. In contrast, those in the wild may associate it with the presence of a new danger or threat. It might be for this reason that animals kept in captivity may express a greater predisposition to perform innovative behaviours (Lehner *et al.*, 2010). However, innovations do not always remain stable over time. A possible explanation for this instability is the presence of conformity within the community, understood as the ability to adapt to the behaviour of the majority to the detriment of a different option (Perry, 2009; Péter *et al.*, 2022). Several studies have documented manifestations where primates living in groups indeed exhibit behaviours of conformity (Miller Greg, 2005; Gunhold *et al.*, 2015; Watson *et al.*, 2018).

Experiments performed by Gunhold *et al.* (2015) showed how common marmoset monkeys exhibit traits of conformism. Individuals were presented with a challenge with two known possible solutions. Most of the marmoset monkeys chose the usual method they performed even when the alternative was more effective. Thus, it was evidenced that group members were able to remember their favourite technique, rather than relying on trial and error techniques to succeed in the task.

Watson *et al.* (2018) found in chimpanzees that minority individuals exhibit a much greater tendency than those in the majority to switch from a pre-existing method to the one presented socially in the group. This occurred even if neither method was more efficient than the other. However, other authors reveal a preference for adopting a new behaviour in some chimpanzees if it is more productive -known as a "copy-if-better" strategy- (Franz & Matthews, 2010; van Leeuwen & Call, 2017).

Miller Greg (2005) mentions an experiment in which innovation becomes a behavioural tradition, leading to conformist behaviours in two sub-populations of chimpanzees. One individual from each subpopulation learned a different method for the same outcome: using a stick to retrieve food from a dispenser. One chimpanzee learned a "lift" technique and the other a "poke" technique. Once they returned to their respective sub-groups, most chimpanzees adopted the imported behaviour. Even those who stumbled upon other methods adjusted to the group's performance.





#### **4.4. Transmission:**

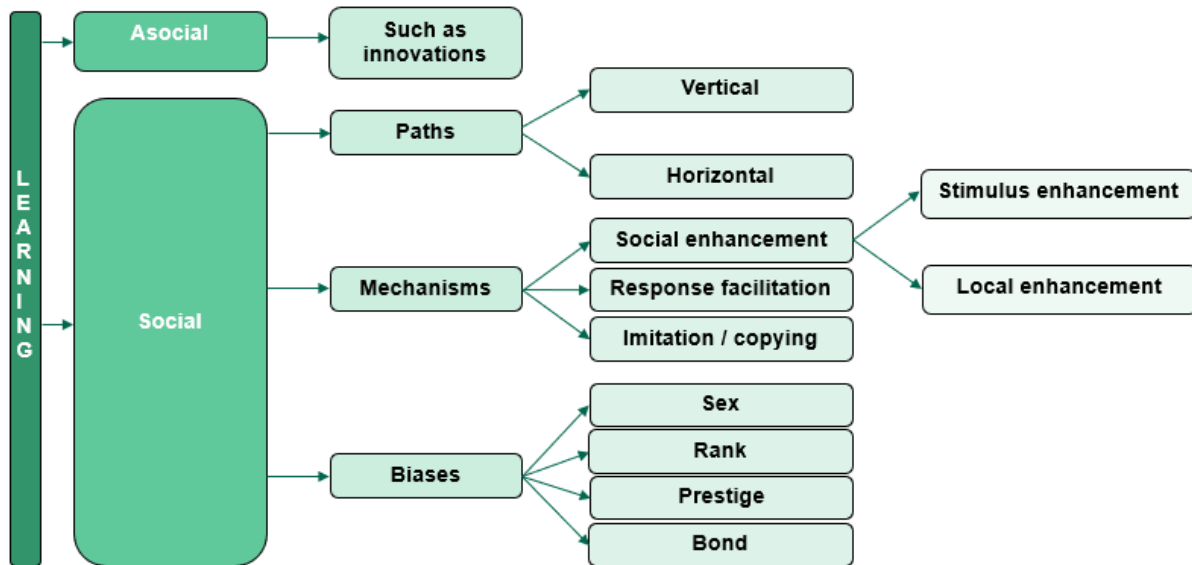
Having explored innovation and conformity within primate culture, we now shift our focus to the study of social transmission, investigating the mechanisms through which these cultural traits are spread among populations.

##### **4.4.1. Asocial and social learning:**

An individual's learning can unfold through two primary pathways: asocial learning and social learning (see Figure 7). The first involves isolated exploration by each individual, unmediated by social influence, and this type of information is obtained through trial and error. The second includes learning related to the social information available in the group, and this kind of knowledge is acquired through various processes (Garcia-Nisa *et al.*, 2023). Socially mediated learning encompasses behavioural changes in naïve individuals through social influence, which can manifest in both direct and indirect forms. Thus, this process can result in: (i) naïve individuals acquiring new skills typical of the group; (ii) the maintenance of the cultural behaviours and emergence of new ones; (iii) convergence of different patterns of behaviour within a group (Huffman *et al.*, 2010).

Tolerance is one of the aspects promoting social learning (Biro *et al.*, 2003; Perry, 2009; Nakamura & Nishida, 2013; Mikeliban *et al.*, 2021; Garcia-Nisa *et al.*, 2023). Chimpanzee mothers tend to show high tolerance towards their offspring. The offspring usually stay closer to their mothers until they are 4 or 5 years old, with the cessation of suckling (Biro *et al.*, 2003). Orangutans similarly display this type of behaviour (Mikeliban *et al.*, 2021). Immature orangutans often beg for food from their mothers. However, the older they get, the less food they request. Interestingly, the mother's tolerance diminishes with both the age of the offspring and the complexity of the task at hand. In general, the more complex the task, the higher the mother's tolerance. Nevertheless, unlike in chimpanzees, the pinnacle of tolerance in orangutans does not align with the weaning age (Mikeliban *et al.*, 2021).





**Figure 7:** Diagram of an individual's learning.

#### 4.4.2. Social learning mechanisms:

There are diverse social learning mechanisms, differing in the level of complexity and the degree of involvement required by the participant(s) (Sinha, 2005). Usually, active teaching is absent (Nakamura & Nishida, 2013). Among the types of socially mediated learning, the most commonly found in this bibliographic review include: social enhancement, response facilitation and imitation or copying.

Examining these mechanisms in more detail, social enhancement can be subdivided into two different categories: stimulus enhancement and local enhancement (Franz & Matthews, 2010). The former occurs when an animal interacts with an object previously used by another individual, regardless of its location. The latter happens when the subject directs its behaviour towards the place where it has observed another individual performing the action (Franz & Matthews, 2010). A representative example is the time spent by juvenile capuchin monkeys near anvils where adults interact to break nuts using stones (Eshchar *et al.*, 2016).

Moving on to another facet, social facilitation, also known as response facilitation, occurs when an individual's performance induces an increased probability of the observer reproducing the same behaviour (Eshchar *et al.*, 2016). A pertinent example is how Balinese long-tailed macaques engage in robbing and bartering





activities approximately 3 minutes after witnessing a demonstrator (Brotcorne *et al.*, 2020).

Imitation, or copying, takes place when an individual learns about a certain behaviour through the observation of another (Sinha, 2005). An illustrative example comes from the chimpanzee community of Sonso in Budongo (Uganda), where an adult male with paralysis of both hands uses lianas to scratch his back. Nonetheless, seven able-bodied chimpanzees also replicated this technique, although it was not indispensable for back scratching (Hobaiter & Byrne, 2010).

#### **4.4.3. Social learning biases:**

The techniques employed by animals for social learning have been called learning and transmission biases or social learning strategies (Tan *et al.*, 2018). Thus, it includes processes for discerning "who" to copy -generally the most skilled individual-, "when" to copy -such as the "copy-when-uncertain" strategy-, or "what" to copy -usually the technique with the greatest reward- (Garcia-Nisa *et al.*, 2023). We can distinguish between two main sources of transmission: vertical and horizontal. Vertical transmission includes mainly learning from the mother, while horizontal or oblique transmission occurs when learning comes from other, usually unrelated, individuals (Tan *et al.*, 2018). In turn, these preferences are shaped by creating different models-based biases present in the group (Tan *et al.*, 2018). These biases are influenced by criteria such as age, sex, rank, prestige, or bonding. Illustrative examples for each bias have been found in this bibliographic review. (Biro *et al.*, 2003; Russon *et al.*, 2007; Perry, 2009; Huffman *et al.*, 2010; Nakamura & Nishida, 2013; Watson *et al.*, 2017; Bono *et al.*, 2018; Tan *et al.*, 2018; Brotcorne *et al.*, 2020).

Biro *et al.* (2003) studied nut-cracking activities in a community of chimpanzees in Bossou, Guinea. Their findings revealed that the subjects typically took as their role models individuals of the same age or older, but not younger than themselves (see Figure 8).





**Figure 8:** An adult female cracks nuts while two juveniles observe her actions closely. There are rows of nuts next to them (*left and up arrows*) (Biro *et al.*, 2003).

Bono *et al.* (2018) focused on the research of vervet monkeys and their payoff- and sex-biased interactions. Their study showed that when confronted with an introduced foraging box (see Figure 9), both male and female individuals significantly copied more female models when the rewards obtained were equal to those acquired by males. Nevertheless, when the rewards obtained by males were higher, the criteria shifted. Male observers switched models, imitating the male, while females displayed fidelity by continuing to copy the female model.



**Figure 9: a.** Adult female opening on the white side of the foraging box; **b.** Adult male opening on the black side of the foraging box (Bono *et al.*, 2018).

Watson *et al.* (2017) demonstrated in groups of captive chimpanzees that individuals preferred to copy dominant models rather than those of lower rank.





However, they statistically observed that when both the group and the model consisted solely of subordinate individuals, social inference was higher. This was not the case when the group was composed of high-ranking chimpanzees.

Tan *et al.* (2018) studied tool-use behaviours in a population of macaques on Koram Island, Thailand. They found that, overall, adult individuals engaged more frequently with conspecifics who employed more effective or rewarding techniques. Meanwhile, young macaques did more independent exploration and interacted with other individuals regardless of the productivity of their techniques.

Nakamura & Nishida (2013) investigated the so-called “Grooming Hand Clasp” behaviour in the Mahale Mountains’ chimpanzee community. Their observations revealed that grooming behaviour was more prevalent among individuals who shared a closer social bond. Likewise, this behaviour was more frequently observed between mothers and offspring (see Figure 10).



**Figure 10:** Grooming Hand Clasp behaviour between a mother and its offspring (Nakamura & Nishida, 2013).

There are other cases that continue to surprise nowadays, like the famous chimpanzee Washoe, studied at the Chimpanzee and Human Communication Institute of the Central University of Washington's State (Cavalieri Paola & Peter Singer, 1993).







This peculiar primate was bred in captivity with human habits from an early age. She was considered the first non-human animal to communicate with our species through human language. Specifically, she learned approximately 350 signs in American Sign Language through which she communicated with humans and other chimpanzees. In addition, she taught this same language to his adopted son Loulis, who in turn taught Dar, a third chimpanzee with whom they lived together. Through observation, researchers confirmed how Washoe showed the ability to have a private conversation with herself through the use of signs; or how Dar played “peek-a-boo” with a rag bear, demonstrating the existence of imagination by substitution in this species (Cavalieri Paola & Peter Singer, 1993). However, these chimpanzees were not the only ones in history to learn American Sign Language. Koko, a gorilla studied at the Stanford University, also came to communicate in this language with her caregiver and other gorillas. Among other things, she displayed self-awareness; understood and used words related to the weather; or resorted to imaginary games involving other hominids (Cavalieri Paola & Peter Singer, 1993).

#### **4.4.4. Tool-use behaviours:**

Most behaviours classified as cultural typically involve tool-use. Nakamura & Nishida (2013) propose that, broadly speaking, the tool-use learning process involves several common steps: (i) initially, the infant begins to express interest in its mother or other adults using tools; (ii) adults usually tolerate the infant's presence and interaction; (iii) attempts are made by the infant through trial and error; (iv) these trial and error processes persist until the individual refines its technique and masters the correct use of the tool. An example of cultural variants for tool-using behaviours was observed by Lamon *et al.*, (2017). They discovered that the chimpanzees of the Sonso community, as previously mentioned, exhibited two behavioural variants related to the use of objects, especially in collecting water from a clay pit. The first subgroup used leaves to ingest the liquid ("clay-pit leaf-spongers"), while the second subgroup used moss to absorb the water ("clay-pit moss-spongers"). Statistical analysis from studies on these chimpanzees estimate that 85-99% of the acquisition of moss-sponging behaviour was through social transmission. However, besides tool-use, there are non-object behaviours that contribute to a group's cultural repertoire. An example is the variation





in grooming behaviours among chimpanzees in the Mahale Mountains, as previously mentioned. The variation in this behaviour lies mainly in the hands involved during grooming (Nakamura & Nishida, 2013).

#### **4.4.5. Animal culture's stability:**

Researchers are engaged in a debate about the factors that explain the stability of animal culture. On the one hand, some argue that mechanisms such as imitation or conformity can ensure fidelity to traditions. On the other hand, others claim that less complex mechanisms such as stimulus enhancement are sufficient to sustain traditions (Franz & Matthews, 2010). Franz & Matthews (2010) put forward this last hypothesis based on a study on capuchin monkeys. The results showed that social enhancement can create and maintain traditions and also induce conformity. Furthermore, they observed that this mechanism can lead to a “copy-when-uncertain” behaviour. This occurs when an individual is unable to obtain sufficient information to solve a task independently and decides to copy it from another conspecific when it seems more profitable. Exploring the elements that underpin the stability of animal culture, Claidière & Sperber (2010) outline 4 factors that contribute to its endurance, beyond various social learning mechanisms: (i) Ecological availability: differences in the environment can contribute to the stabilization of traditions. A representative case is the use of sticks in chimpanzees to collect ants, as previously mentioned; (ii) Reward-based factors: the presence of a reward reinforces the performance of a behaviour. An example of this is the ingestion of certain leaves in chimpanzees that allow them to expel intestinal parasites; (iii) Content-based factors: the complexity of behaviour can make it easier or more difficult to learn, contributing or not to its diffusion; (iv) Source-based factors: depending on from whom the behaviour has been learned, there may be different levels of fidelity.

#### **4.5. Studying methods:**

Various analytical methods assist in comprehending the dynamics of animal culture and how to detect them. One of the main statistical methods mentioned in the





studies of this bibliographic is the method of exclusion or ethnographic method. This approach acts as an initial step for investigations seeking to determine if a behaviour results from factors associated with social learning mechanisms. Therefore, it aims to exclude variability based on purely genetic or environmental factors (Neadle *et al.*, 2017). It also gains statistical power when intraspecific populations share the same ecological niche (van Leeuwen *et al.*, 2018). Nevertheless, it is unable to detect the types of social learning that are at play (Neadle *et al.*, 2017). Thus, this method is generally used to detect cultural differences between populations, as it cannot identify all cultural variants present between groups (Gruber *et al.*, 2009). Hence, it should complement other methods searching for additional evidence of social learning (Perry, 2009).

The method of exclusion generates some debate as it struggles to clearly explain the cognitive processes derived from social learning (Lamon *et al.*, 2017). Some authors criticize that animal culture is seen as the residual product of a process of eliminating genetic and environmental factors (van Leeuwen *et al.*, 2018). Laland & Janik (2006) suggest that these factors have a greater influence than assumed in traits classified as cultural. On the one hand, animal culture is an adaptive behaviour to take advantage of the resources offered by the environment. On the other hand, there is a covariance between genetics and culture, as the learning of cultural behaviours is influenced by genetic predispositions and aptitudes. Lycett *et al.* (2010) highlight that some behaviours classified as cultural through this method have been studied only within subspecies to rule out genetic influence. In turn, genetic studies reveal that, in some cases, these subspecies have been genetically isolated for hundreds of thousands of years, potentially giving rise to genetic variations that could explain the performance of certain behaviours. The method of exclusion may therefore lead to false positive behaviours classified as cultural (Nakamura & Nishida, 2013). Laland & Janik (2006) suggest that the problem in the debate is not whether a behaviour depends on social or asocial learning, but rather how much of the variance is attributed to social learning. Thus, they propose that a promising solution may lie in field experiments, such as exchanging individuals between populations or entire populations between ecological niches. However, they acknowledge that this method is not feasible at ethical levels, especially in primates. Nonetheless, it could be carried out with captive animals, for example by exchanging habitats where they are kept. The





debate seems to be ongoing, but a plausible explanation might involve the interplay between these three factors: genetics, environment and culture (Nakamura & Nishida, 2013).

Other methods have emerged over time, including Network-Based Diffusion Analysis (NBDA), a statistical method for inferring social learning in a group of individuals. One of its premises is that social transmission should be faster among individuals who share a closer bond (Garcia-Nisa *et al.*, 2023). This method is also able to measure the influences of other factors linked to social learning such as sex, age, or rank, which significantly reduce the number of false positives (Hoppitt & Laland, 2011). In addition, the method has been extended to cover additional considerations, such as the order or time in which individuals acquired a new trait. These complements are called Order of Acquisition Diffusion Analysis (OADA) and Time of Acquisition Diffusion Analysis (TADA) (Garcia-Nisa *et al.*, 2023). However, the NBDA method is unable to infer social learning in each specific behavioural variant, focusing instead on the task as a whole (Kendal *et al.*, 2010).

Kendal *et al.* (2009) propose an alternative method distinguishing between asocial learning and social learning, known as the option-bias method. It is able to study the frequency of behavioural variants exhibited in a particular ecological niche, applying to natural, semi-natural and captive animal groups. On the one hand, asocially learned behaviours are expected to diminish homogeneity within a population as each individual might express a different variant of the behaviour. On the other hand, socially learned behaviours are expected to increase homogeneity as individuals tend to converge in the same behavioural variant. Thus, this method is particularly effective in inferring social learning for those behaviours displayed through various options where group homogeneity is expected (Kendal *et al.*, 2010). To apply this method, Kendal *et al.* (2009) claim that the researcher is required to independently (i) know the genetic differences between populations; (ii) assess environmental differences that may predispose to perform variants based on asocial learning; (iii) distinguish the behavioural options present in the group; (iv) delimit the population in which behavioural homogenisation is expected to occur. The option-bias method offers the advantage of detecting social learning with greater significance compared to other conventional statistical methods. Moreover, its validity has been corroborated through





various experimental databases (Huffman *et al.*, 2010). Nonetheless, this method is not applicable when there is genetic or environmental heterogeneity; nor is it suitable when social learning is not expected to result in behavioural homogeneity (Kendal *et al.*, 2009).





## 5. CONCLUSIONS

**First:** The boundaries for defining whether a behaviour can be considered cultural or not are blurred, and there is still debate within the scientific community as to what criteria make up the definition of animal culture.

**Second:** Through this bibliographic review we can corroborate that culture is not an exclusively human trait, as we have it in common with other taxa, and that we share similar features of culture to those present in other primates.

**Third:** Behaviours classified as cultural always have a part of the variability explained by the influence of genetics or the environment, understanding that cultural behaviours are so because of an intertwining of culture, genetics and environment in different extensions.

**Fourth:** Transmission through social learning may take place through various mechanisms -such as social enhancement, response facilitation or imitation- and biases based on different criteria -such as age, rank, sex or bonding-.

**Fifth:** Behavioural innovations arise mainly through migrant females and juveniles, even when conformist behaviours may occur, contributing to the fluidity and emergence of animal culture.

**Sixth:** The similarities observed between the culture of non-human primates and our own bring us closer together as rational, sentient species. Their complexity reminds us of the commitment humans bear to ensure the welfare of these animals and to conserve and protect the natural environment they inhabit.

**Seventh:** Various methods of statistical analysis exist to determine theoretically whether a behaviour can be classified as cultural or is influenced by social learning. These methods can complement each other and potentially more effective methods have yet to be developed.





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