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Effect of captivity on cultural transmission in Great Apes

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Abstract

Cultural transmission, as an alternative mode of information transfer to genetic inheritance, plays a vital role in enhancing the adaptability and efficiency of individual and group behaviours. Social learning mechanisms facilitate the transmission of individual innovations, resulting from individual learning, across group members and generations. Recent studies have indicated that animals in captivity exhibit reduced neophobia and higher capacities for individual innovation. However, the impact of captivity on the transmission of these innovations through social learning remains unclear. Here, I have reviewed the existing literature on social learning in wild and captive great apes, as these studies provide the most abundant data for drawing comparisons. I examined how reduced proximity and higher tolerance among individuals in captivity could potentially contribute to variations in social learning capacities between these two settings. In addition, I have highlighted the importance of research on social learning and cultural transmission in captive animals for the development of effective conservation policies. Furthermore, I have discussed the role of zoological institutions in supporting these research efforts.

Introduction

The discovery of culture-like phenomena in wild animals, particularly great apes, is a relatively recent development (van Schaik et al., 2003; Whiten et al., 1999, 2001). Evidence for culture has been observed exclusively in groups of animals that live in identical environments and share indistinguishable genetic makeup (Gruber et al., 2012; Krützen et al., 2011; Luncz et al., 2012). In the absence of ecological and genetic differences, the emergence of group-specific behaviours has been attributed to the capacity for social learning. Suggesting that animal behaviours may be 'cultural' and can be transmitted socially across generations (Whiten, 2005, 2017a). Although the precise definition of culture remains a subject of debate (Gruber et al., 2015), most anthropologists and primatologists widely accept the definition proposed by Reader and Laland (2003). They define culture as 'group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information'. This comprehensive explanation not only allows us to draw meaningful comparisons between human and animal cognition but also implies the importance of social learning in the formation of culture.

Although it is particularly prominent in humans, social learning is a widespread phenomenon in the animal kingdom (Allen et al., 2013; Jaeggi et al., 2010; R. L. Kendal et al., 2010; Samuni et al., 2014). The advantages of social learning are evident as it allows individuals to reduce the costs and risks associated with individual innovations by adopting beneficial practices from others (Giraldeau et al., 2002; R. L. Kendal et al., 2018; Laland, 2004). Moreover, social learning strategies are believed to have evolved to guide the utilization and transmission of social information, helping individuals avoid adopting costly or suboptimal behaviours. Studies on social learning in apes offer valuable insights into the cognitive capacities of these animals and the evolution of human cognition and culture (Whiten, 2011). By exploring social learning in apes, we gain unique opportunities to understand the intricacies of their cognitive abilities and how they relate to human cultural development. These studies also challenge the notion of human culture's exclusivity, prompting us to recognize the continuum of cultural behaviours across species and the complexities of social learning in diverse animals.

Social learning biases and mechanisms in Great Apes

Social learning biases

While social learning is generally considered to provide direct adaptive advantages, it may not always be beneficial. Indiscriminate social learners run the risk of adopting costly or suboptimal behaviours (R. L. Kendal et al., 2005; Laland & Williams, 1998). Hence, being selective in choosing when and from whom to engage in social learning becomes crucial. Considering this, researchers propose that social dynamics within groups likely give rise to biases in social learning, which can help individuals select the most productive behaviour (Giraldeau et al., 2002; Laland, 2004). In this discussion, I described several learning biases that have been extensively researched in great apes (Haun et al., 2012; Matsuzawa et al., 2001; van de Waal et al., 2013, 2014; van Leeuwen & Haun, 2013; Waal et al., 2012). These biases fall into two categories- frequency-based biases and model-based biases (Watson et al., 2018).

Frequency-based bias

Frequency-based biases refer to the inclination of individuals to align their attitudes with the majority (Asch, 1956; Cialdini & Goldstein, 2004), sometimes even disregarding their pre-existing preferences in favour of the majority's preference (van de Waal et al., 2013; Whiten et al., 2005). Open diffusion studies are often used to examine how information or innovations spread through the population. This involves introducing novel behaviours to a few individuals within a group, and then observing how the behaviour spreads and is transmitted to other group members over time. The design is labelled open since it leaves the decision of naïve individuals to select who they will watch and who they will copy (Whiten, 2017b). In the study by Whiten et al. (2005), chimpanzees were provided with puzzle boxes that could be opened using either one of two techniques. One high-ranking female from each of the two groups was trained in one of two techniques, and then she demonstrated this method for opening the puzzle box to the rest of her group members. After a short period, researchers found that although some individuals opened the box using alternative methods, individuals were more likely to converge on the option that was most common within the groups. However, other researchers have suggested that the chimpanzees simply returned to their original method after a period of exploration (van Leeuwen & Haun, 2013). The evidence for such conservative problem-solving is somewhat mixed, as some studies suggest that individuals are more inclined to stick to familiar methods that have been successful in the past (Harrison & Whiten, 2018; Hopper et al., 2011; Hrubesch et al., 2009), while others have documented greater flexibility (Hopper et al., 2015).

In a following study by Watson et al. (2018), the majority of the groups were trained on one method for opening a puzzle box and the minority was trained on an alternate method. They observed that the minority rapidly converged onto that method used by the majority. This would again be indicative of conformity. However, it is particularly challenging to discern whether decisions are made solely based on the choice of the majority (informational conformity) or if they result from social awareness and the desire to conform to the group (normative conformity) (Claidière & Whiten, 2012; Deutsch & Gerard, 1955; van Schaik, 2012).

In a token exchange task, van Leeuwen and Haun (2013) found that individuals were motivated to switch to methods that awarded greater rewards, rather than conforming to the majority. In another study by Vale et al. (2017), researchers trained captive chimpanzees to prefer one colour of food and then moved them to a group with strong preferences for a different colour of food. The exchanged group did not conform to the foraging preferences of the new group. Therefore, it is possible that conformity might not always be the norm in apes, and without systematic testing, we cannot be sure whether the outcome is driven by majority biases or some other biases.

Researchers argue that individuals may direct their social learning towards specific individuals who are perceived as more successful or knowledgeable, rather than being influenced solely by the behaviour displayed by the majority (Haun et al., 2013; van Leeuwen & Haun, 2013). This suggests that social learning might be more nuanced and individual-focused, rather than simply driven by the choices of the majority.

Model-based bias

Model-based biases in social learning refer to the influence of characteristics of the individual providing information (known as the model or demonstrator), on the learner's use of social information (Laland, 2004; Wood et al., 2013). By adopting behaviours based on specific model characteristics, individuals can maximize the benefits of social learning, as some models may offer more relevant or advantageous information than others. Various characteristics have been proposed for this purpose, including age, sex, rank, and previous experience.

Rank-based bias in social learning may arise if an individual's rank serves as a proxy for success, in which case adopting behaviours of higher-ranking individuals could be beneficial. Studies with captive chimpanzees of different ages and ranks, trained on reward-based tasks, have found evidence supporting learning biases towards copying dominant and knowledgeable individuals (Horner et al., 2010). However, these findings lack corroboration from field studies. In chimpanzees, it has been observed that there is a relatively high level of innovation compared to the number of traditions that exist within the group (Nishida et al., 2009). It has been explained that although low-ranking individuals performed more innovations compared to high-ranking individuals (Reader & Laland, 2003), bias towards copying higher-ranking individuals might be responsible for the discrepancies between the number of innovations and the established traditions in the chimpanzee group (R. Kendal et al., 2015). This has further been supported by more recent studies. In a study by Horner et al. (2010), two females from each of the two groups of captive chimpanzees were trained to deposit tokens in different receptacles in exchange for rewards. For both groups, one of the two models was older than the other, higher ranking and had previously introduced novel tasks to the group. The collection of traits was labelled as 'prestige'. After the models demonstrated their methods to naïve observers, more tokens were deposited in the receptacle demonstrated by the 'prestige' female than the one demonstrated by the 'non-prestige' female. This study, however, only provided limited support for rank-bias, because in addition to rank age and previous success rate of the 'prestige' female also might have influenced the decision of observers. Following this another study investigated the diffusion of behaviours in a foraging task. In this study, models could be of lower, same, or higher rank, than the naïve learners. The findings indicated that the individuals were more likely to copy models that were higher, rather than lower or the same rank as themselves (R. Kendal et al., 2015).

In field studies on chimpanzees and orangutans, another form of social bias has been observed. Kinship-based bias between mothers and infants has commonly been observed in both these species (Jaeggi et al., 2010; Matsuzawa et al., 2001; Schuppli et al., 2016). Mothers act as primary models for their infants during early life. Field experiments on tool use in chimpanzees have shown that infants are significantly more likely to observe behaviour of novel behaviours, compared to other juveniles or adults (Biro et al., 2003). Other studies have also suggested that there may be a link between age and the ability to acquire new novel behaviours, called the sensitive learning period. During these sensitive learning periods, individuals are more likely to take up new novel behaviours (Bandini et al., 2021; Matsuzawa et al., 2001). Likewise, research conducted on orangutans has revealed that infant orangutans show heightened levels of "peering" behaviour directed towards their mothers when their mothers are engaged in complex foraging tasks (Jaeggi et al., 2010; Schuppli et al., 2016).

Preference of kin as the model has been suggested to have emerged due to increased tolerance from mothers towards infants, allowing for greater learning opportunities for infants to learn novel behaviours (Coussi-Korbel & Fragaszy, 1995).

In addition, to kinship-based bias, sex-based bias which has been documented in wild vervet monkeys (van de Waal et al., 2010), has also been suggested to exist in apes. The sex-based bias has been explained to emerge due to selective attraction towards individuals based on their sex. Orangutans have been suggested to display sex-based biases in social learning. This is because female orangutans tend to be philopatric, remaining in their birth area, while male orangutans have wide-ranging (Singleton et al., 2008). Thus, males are less likely to spread socially learned information related to localized traditions. Further, recent studies have demonstrated immature females direct most attention towards mothers, whereas immature males show attentional preferences towards individuals other than their mothers (Ehmann et al., 2021).

Social learning mechanisms

The mechanism of social learning elucidates how information is transmitted from a model to a learner. Social learning mechanisms range from basic forms of social learning such as local or stimulus enhancement, to more complex mechanisms such as copying (Heyes, 1994). Simpler forms of social learning include stimulus or local enhancement, where a learner's attention is drawn towards an object or location due to the actions or presence of another individual. In this case, the learner acquires new behaviours without directly replicating the actions but rather using its existing behavioural resources (Whiten, 2017b). Additionally, researchers have identified two principal types of copying mechanisms - imitation and emulation. Imitation involves learning by copying the form of others' actions, while emulation focuses on acquiring desirable environmental results from others' actions (Tomasello et al., 1987; Whiten et al., 2004).

Previously, it was argued that human culture results primarily from imitation and teaching, which involve more complex cognitive processes compared to emulation observed in animal cultures, which require "lower-level" social learning (Galef, 1992; Laland & Galef, 2009; Tomasello, 1990, 2009). However, later studies have provided evidence for imitation in chimpanzees through various tests that require matching of actions (Buttelmann et al., 2007; Custance et al., 1995). Additionally, studies in captive chimpanzees have shown flexible use of imitation and emulation (Hopper et al., 2008). The tested chimpanzees were observed to imitate actions when presented with complex tasks (Byrne & Russon, 1998) while displaying more emulative responses when they are made aware that certain actions might be redundant and not copied (Horner & Whiten, 2005). Although, other studies have indicated there might be limitations to the ability for imitation in chimpanzees (Fuhrmann et al., 2014; Tennie et al., 2012; Tomasello et al., 1997). Despite mixed stances among researchers regarding whether apes can imitate behaviour, an important discovery from cultural diffusion experiments is that apes can transmit and maintain traditions, regardless of whether these processes are driven by imitative or emulative copying mechanisms (Bandini & Tennie, 2017; Whiten et al., 2016).

Culture in Apes

The earliest studies on ape culture primarily focused on observing wild apes (van Schaik et al., 2003; Whiten et al., 1999, 2001). Researchers examined group differences in behaviours (referred to as cultural variants) that were present in some locations but absent in others, without considering ecological factors. This is known as the method of exclusion and has been similarly used by studies on human and pre-modern hominins, for the identification of culture (de la Torre, 2019; Stout et al., 2019). Cultural variants in ape studies encompassed various activities from tool use for foraging (like

termite fishing or nut-cracking) (Boesch et al., 1994; Hirata et al., 2009; Lonsdorf et al., 2004), to social interactions (such as hand clasp grooming) (McGrew & Tutin, 1978).

In addition to adopting novel behaviours from others, the concept of cumulative culture was introduced to explore the ability of individuals to modify behaviours and flexibly switch to more optimal alternatives (Davis et al., 2016). Cumulative cultures arise from individuals' ability to build upon existing culturally transmitted behaviours, either by applying existing behaviours in new contexts or by developing entirely new behaviours (Gruber et al., 2015). Over time, repeated modifications lead to cultural traits that are too complex to have been invented by a single individual. Researchers emphasize that regardless of the rate of innovation, cumulative changes cannot emerge without accurate transmission of knowledge from one generation to the next. As a result, some researchers initially proposed that cumulative culture was unique to humans (Dean et al., 2014; Galef, 2009). Later studies have argued that apes exhibit basic cumulative phenomena, a notion supported by research conducted on tool use in various species and groups of apes, both in the wild (Boesch et al., 1994; Matsuzawa et al., 2001; Sanz & Morgan, 2007) and in captive chimpanzees (Yamamoto et al., 2013) and orangutans (Lehner et al., 2011). However, since these behaviours have not conclusively been shown to result from successive modifications onto ancestral forms, nor do they rely on copying to be transmitted across individuals and over generations (Dean et al., 2014; Mesoudi & Thornton, 2018; Tennie et al., 2009).

The existence of cumulative cultures in great apes is still a matter of ongoing debate. Human cumulative culture, which is thought to have emerged through teaching and imitation (Dean et al., 2014; Galef, 2009), may either be completely absent in great apes or not present to the same extent as in humans (Musgrave et al., 2016; Tennie et al., 2012). It has been further argued that human culture is generally opaque and requires knowledgeable individuals to specifically instruct naïve learners (Csibra & Gergely, 2009). While culture in non-human apes is transparent and does not necessarily require instruction to be acquired (Pradhan et al., 2012). Therefore, researchers have suggested that the differences in social learning mechanisms might not be sufficient for explaining the emergence of cumulative culture (Yamamoto et al., 2013).

As a result, further research is necessary to gain a deeper understanding of the extent of cumulative behaviour in the animal kingdom. By exploring the concept of cumulative culture across various species, researchers can gain valuable insights into the mechanisms of cultural evolution and the role of social learning in accumulating knowledge and complexity within societies. Recognizing the presence of cumulative culture beyond humans broadens our understanding of the cognitive capabilities and cultural dynamics within diverse animal communities.

Discussion

Recently, there has been a shift in research focus towards studying apes and other non-human primates in captive settings, where genetic and environmental factors contributing to group differences can be more clearly eliminated. The findings from these studies suggest that animals in natural and captive environments show measurable cognitive differences (Forss et al., 2015; Rössler et al., 2020; van Schaik et al., 2016). Animals in captivity have been demonstrated to be more curious and innovative (Benson-Amram & Holekamp, 2012; Gruber et al., 2012; Kummer & Goodall, 1985; Rössler et al., 2020; Shumaker et al., 2011), a phenomenon referred to as 'captivity bias' (Haslam, 2013). Researchers have speculated that reduced neophobia (fear of new things) and increased free time in captive environments contribute to this heightened explorative tendency (Barnett, 1958; Greenberg, 2003; Mettke-Hofmann et al., 2002). While these studies explore the

impact of captivity on the capacity for individual innovation (or individual learning), little is known about its effect on social learning, and subsequently on the transmission of culture.

Here, I have discussed the influence of captivity on both individual and social learning and its implications for cultural transmission in great apes. Through this exploration, I aim to generate hypotheses that can be tested out in future studies to gain deeper insights into the complexities of ape culture. Further, I discuss the crucial role played by zoological institutions in facilitating future research on cultural transmission in apes. Lastly, I discuss how the findings from studies on great ape culture and social learning mechanisms can help inform and shape policies concerning the conservation of these remarkable animals.

Proposed effects of captivity on the individual (learning) innovation

Numerous studies investigating cognitive abilities in non-human animals have focused on their response to novelty, as it is considered a significant factor driving innovation of novel behaviours (A. B. Kaufman et al., 2011; J. C. Kaufman & Kaufman, 2004; Reader & Laland, 2003). Novelty response can be described as either neophilia, involving exploration of novelty, or neophobia, indicating the avoidance or fear of novelty (Greenberg, 2003, 2003; Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2002; Russell, 1973; Sabbatini et al., 2007). Marked differences have been observed between wild and captive apes in their response to novel objects, often referred to as the captivity effect or bias (Forss et al., 2015; Haslam, 2013). The increased tendency to explore in captivity is attributed to the reduced predation pressures and foraging challenges, allowing captive animals more time for exploration (Benson-Amram & Holekamp, 2012; Kummer & Goodall, 1985). Apes in the wild cannot know whether novel objects are dangerous and therefore benefit from being conservative (Wich et al., 2004). On the other hand, zoo-living animals tend to overcome their initial neophobia towards novel objects as they have positive experiences with them.

In addition to this, intrinsic neophobia can be overcome using social information (Forss et al., 2017). Firstly, the presence of other individuals reduces the risk of approaching novel objects because vigilance can be shared among group members, and the cost of paying attention to and exploring novel objects is lower as well. Secondly, naïve individuals can rely upon experienced individuals that are familiar with objects and have developed novel methods for interacting with novel objects. Thus, the presence or association with experienced parents or models can facilitate the exploration of novelty by naïve learners who might exhibit high intrinsic neophobia. Experiments conducted in captive apes have supported these findings. Neophobia was overcome faster in social settings compared to solitary conditions. When all individuals were equally naïve, social attention towards group members was the main factor influencing the decision to approach novelty (Jaeggi et al., 2008, 2010; van Schaik et al., 2003). Due to the limited diversity in captivity, captive apes are more likely to be familiar with objects or have previous experience with them. As a result, the use of social information to overcome neophobia can be more prevalent in captivity than in the wild.

Potential effects of captivity on social learning and culture transmission

Despite the presence of many innovations within a group, social learning biases may only allow for the transmission of a few of these innovations from demonstrators or models to learners (Coussi-Korbel & Fragaszy, 1995). As a result, the frequency of innovation might not be directly relevant to the establishment of these innovations as cultural traits. Therefore, it is essential to shift our focus from individual innovation and instead investigate the effects of captivity on social learning and the transmission of cultures. In the absence of comprehensive literature on this topic, I present arguments for the potential effects of captivity on social learning, which can be formulated into formal hypotheses for testing in future studies.

Firstly, due to the restricted group members within an enclosure, stimulus or local enhancement becomes more apparent. Less neophobic apes in captivity are more likely to explore novelty, while more neophobic apes are more likely to observe the behaviours of others. The proximity in captivity is likely to provide more opportunities for social learning and facilitate more accurate copying of behaviours. Additionally, the benefits of actions may be more transparent, making individuals more likely to adopt behaviours from others that are more rewarding. Although, some researchers have also proposed that apes may have sensitive learning periods during which they are more likely to adopt novel behaviours, and beyond this period, individuals are less likely to acquire new behaviours and stick to existing behavioural repertoire even if they are less beneficial (Bandini et al., 2021; Motes-Rodrigo & Tennie, 2022). Thus, in addition to benefits conferred by closer proximity to conspecifics, the age of learners and peers may also play an important role in the transmission of novel behaviours.

The second line of argument pertains to the accuracy of information transfer in wild and captive settings. Individuals with prior experience or training on a specific task tend to be more successful and often end up becoming models for naïve learners (Horner et al., 2010; Reader & Laland, 2003; Watson et al., 2017). However, the ability of naïve learners to copy actions from trained or knowledgeable individuals can be thought to be different in the two settings. The crucial difference between the two lies in the opportunities for participating in the task and, more importantly, the opportunities for observing demonstrators. In this regard, captive apes benefit from having more frequent social learning opportunities and might be more likely to successfully transmit complex tasks. Additionally, while it is debatable whether human or conspecific models are better for learners (De Waal et al., 2008), captive apes benefit from being able to observe both types of models.

To summarize, I hypothesize that captive apes benefit from high-fidelity transmission of behaviours and information due to closer proximity with conspecifics. Further, captive apes are more likely to adopt (or even build on) new behaviours that are more optimal because the benefits of actions are more transparent in captivity. Furthermore, captive apes might be capable of transmitting more complex tasks than their wild counterparts due to higher opportunities for social learning. I believe that future studies investigating these effects of captivity on social learning might be crucial in improving our understanding of ape culture and cognition.

Importance of research in zoological institutions

Zoological institutes play a crucial role in investigating the individual and social learning capacity of captive great apes. Research in zoological institutions offers opportunities to manipulate various aspects of social learning, allowing researchers to disentangle the effects of different factors. Conducting tests on individuals and groups and controlling the information made available to specific individuals provides valuable insights into the influence of group settings on innovation probability (Amici et al., 2014). Moreover, the ability to control environmental factors ensures that findings from experiments with different groups are comparable.

Further, keepers in these institutions are often made to maintain records of past experiences and life histories of the housed animals, providing invaluable information for cognition researchers investigating the learning mechanisms underlying behaviour acquisition. Naivety and past experiences can significantly impact individual performance in experiments, making these records essential for assessing learning abilities accurately. Furthermore, information about the rearing background of animals is particularly valuable in evaluating their learning abilities.

Therefore, research on great apes in captive settings presents a unique and controlled environment that allows for comprehensive studies on cognition and social learning, leading to a deeper understanding of the cognitive capacities and behaviours of these remarkable animals.

Relevance of culture for conservation of Great Apes

Researchers have suggested that while many behaviours can be individually re-innovated across populations, some unique behaviours are acquired through social learning and are restricted to specific geographic areas (Motes-Rodrigo & Tennie, 2022). These culturally-dependent behaviours become vulnerable to disappearing if the populations that possess them face threats or habitat destruction. Thus, conservation efforts for great apes should focus on protecting these locally restricted behaviours. These culturally-dependent behaviours are less likely to be individually re-innovated in other populations, making them susceptible to loss if their habitats are endangered or destroyed. Prioritizing the protection of populations with unique and culturally important behaviours can contribute significantly to the conservation of great ape cultures and safeguarding their distinctive behavioural heritage.

Conservation efforts need to recognize not only the genetic diversity within populations but also the distinct cultural aspects that make each group unique. The integration of cultural components of heritable variation is essential for maintaining evolved adaptation and heritable variation in natural populations. Preservation of both behavioural diversity and culturally dependent behaviours is vital to ensure the long-term survival of great apes in the face of various environmental challenges and human impacts. Consequently, a comprehensive understanding of cultural processes in apes serves as a powerful tool in formulating effective conservation policies and practices.

Conclusion

In conclusion, research on the cognition of captive apes is of paramount importance for various reasons. Firstly, it allows us to compare their cognitive abilities and behaviours with those of their wild counterparts, shedding light on the potential effects of captivity on their cognition. Secondly, understanding the cognitive capacities of captive apes is crucial for their conservation and welfare, as it helps in designing enriching environments and implementing effective welfare practices to ensure their well-being. Additionally, captive settings provide controlled environments for behavioural research, enabling scientists to investigate social learning, problem-solving, communication, and other aspects of great ape behaviours. Moreover, studying cultural transmission in captive apes offers unique insights into how individuals learn and pass on behaviours, contributing to our understanding of cultural traditions in these animals. By considering all these aspects, research on great ape culture in captive species plays a vital role in enhancing our understanding of these remarkable beings, promoting their conservation, and ensuring their overall welfare in human care.

References

- Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales. *Science*, *340*(6131), 485–488. <https://doi.org/10.1126/science.1231976>
- Amici, F., Aureli, F., & Call, J. (2014). Response facilitation in the four great apes: Is there a role for empathy? *Primates; Journal of Primatology*, *55*(1), 113–118. <https://doi.org/10.1007/s10329-013-0375-1>
- Asch, S. E. (1956). Studies of independence and conformity: I. A minority of one against a unanimous majority. *Psychological Monographs: General and Applied*, *70*(9), 1–70. <https://doi.org/10.1037/h0093718>
- Bandini, E., Motes-Rodrigo, A., Archer, W., Minchin, T., Axelsen, H., Hernandez-Aguilar, R. A., McPherron, S. P., & Tennie, C. (2021). Naïve, unenculturated chimpanzees fail to make and use flaked stone tools [version 2; peer review: 3 approved]. *Open Research Europe*, *1*, 20. <https://doi.org/10.12688/openreseurope.13186.2>
- Bandini, E., & Tennie, C. (2017). Spontaneous reoccurrence of “scooping”, a wild tool-use behaviour, in naïve chimpanzees. *PeerJ*, *5*, e3814. <https://doi.org/10.7717/peerj.3814>
- Barnett, S. A. (1958). Experiments on ‘Neophobia’ in Wild and Laboratory Rats. *British Journal of Psychology*, *49*(3), 195–201. <https://doi.org/10.1111/j.2044-8295.1958.tb00657.x>
- Benson-Amram, S., & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4087–4095. <https://doi.org/10.1098/rspb.2012.1450>
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition*, *6*(4), 213–223. <https://doi.org/10.1007/s10071-003-0183-x>
- Boesch, C., Marchesi, P., Marchesi, N., Fruth, B., & Joulian, F. (1994). Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution*, *26*(4), 325–338. <https://doi.org/10.1006/jhev.1994.1020>
- Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science*, *10*(4), F31-38. <https://doi.org/10.1111/j.1467-7687.2007.00630.x>
- Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *The Behavioral and Brain Sciences*, *21*(5), 667–684; discussion 684-721. <https://doi.org/10.1017/s0140525x98001745>
- Cialdini, R. B., & Goldstein, N. J. (2004). Social influence: Compliance and conformity. *Annual Review of Psychology*, *55*, 591–621. <https://doi.org/10.1146/annurev.psych.55.090902.142015>
- Claidière, N., & Whiten, A. (2012). Integrating the study of conformity and culture in humans and nonhuman animals. *Psychological Bulletin*, *138*(1), 126–145. <https://doi.org/10.1037/a0025868>
- Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*(6), 1441–1453. [https://doi.org/10.1016/0003-3472\(95\)80001-8](https://doi.org/10.1016/0003-3472(95)80001-8)
- Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences*, *13*(4), 148–153. <https://doi.org/10.1016/j.tics.2009.01.005>

- Custance, D. M., Whiten, A., & Bard, K. A. (1995). Can young chimpanzees (*Pan troglodytes*) imitate arbitrary actions? Hayes & Hayes (1952) revisited. *Behaviour*, *132*(11–12), 837–859. <https://doi.org/10.1163/156853995X00036>
- Davis, S. J., Vale, G. L., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2016). Foundations of cumulative culture in apes: Improved foraging efficiency through relinquishing and combining witnessed behaviours in chimpanzees (*z*). *Scientific Reports*, *6*(1), Article 1. <https://doi.org/10.1038/srep35953>
- de la Torre, I. (2019). Searching for the emergence of stone tool making in eastern Africa. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(24), 11567–11569. <https://doi.org/10.1073/pnas.1906926116>
- De Waal, F. B. M., Boesch, C., Horner, V., & Whiten, A. (2008). Comparing Social Skills of Children and Apes. *Science*, *319*(5863), 569–569. <https://doi.org/10.1126/science.319.5863.569c>
- Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2014). Human cumulative culture: A comparative perspective. *Biological Reviews of the Cambridge Philosophical Society*, *89*(2), 284–301. <https://doi.org/10.1111/brv.12053>
- Deutsch, M., & Gerard, H. B. (1955). A study of normative and informational social influences upon individual judgment. *The Journal of Abnormal and Social Psychology*, *51*(3), 629–636. <https://doi.org/10.1037/h0046408>
- Ehmann, B., Schaik, C. P. van, Ashbury, A. M., Mörchen, J., Musdarlia, H., Atmoko, S. U., Noordwijk, M. A. van, & Schuppli, C. (2021). Immature wild orangutans acquire relevant ecological knowledge through sex-specific attentional biases during social learning. *PLOS Biology*, *19*(5), e3001173. <https://doi.org/10.1371/journal.pbio.3001173>
- Fors, S. I. F., Koski, S. E., & van Schaik, C. P. (2017). Explaining the Paradox of Neophobic Explorers: The Social Information Hypothesis. *International Journal of Primatology*, *38*(5), 799–822. <https://doi.org/10.1007/s10764-017-9984-7>
- Fors, S. I. F., Schuppli, C., Haiden, D., Zweifel, N., & van Schaik, C. P. (2015). Contrasting responses to novelty by wild and captive orangutans. *American Journal of Primatology*, *77*(10), 1109–1121. <https://doi.org/10.1002/ajp.22445>
- Fuhrmann, D., Ravnani, A., Marshall-Pescini, S., & Whiten, A. (2014). Synchrony and motor mimicking in chimpanzee observational learning. *Scientific Reports*, *4*(1), Article 1. <https://doi.org/10.1038/srep05283>
- Galef, B. G. (1992). The question of animal culture. *Human Nature*, *3*(2), 157–178. <https://doi.org/10.1007/BF02692251>
- Galef, B. G. (2009). Culture in animals? In *The question of animal culture* (pp. 222–246). Harvard University Press. <https://doi.org/10.1007/BF02692251>
- Giraldeau, L., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1427), 1559–1566. <https://doi.org/10.1098/rstb.2002.1065>
- Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. In *Animal innovation* (pp. 175–196). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780198526223.003.0008>
- Greenberg, R., & Mettke-Hofmann, C. (2001). Ecological Aspects of Neophobia and Neophilia in Birds. *Current Ornithology*, *16*. https://doi.org/10.1007/978-1-4615-1211-0_3
- Gruber, T., Potts, K. B., Krupenye, C., Byrne, M.-R., Mackworth-Young, C., McGrew, W. C., Reynolds, V., & Zuberbühler, K. (2012). The influence of ecology on chimpanzee (*Pan troglodytes*) cultural

- behavior: A case study of five Ugandan chimpanzee communities. *Journal of Comparative Psychology (Washington, D.C.: 1983)*, 126(4), 446–457. <https://doi.org/10.1037/a0028702>
- Gruber, T., Zuberbühler, K., Clément, F., & van Schaik, C. (2015). Apes have culture but may not know that they do. *Frontiers in Psychology*, 6. <https://www.frontiersin.org/articles/10.3389/fpsyg.2015.00091>
- Harrison, R. A., & Whiten, A. (2018). Chimpanzees (*Pan troglodytes*) display limited behavioural flexibility when faced with a changing foraging task requiring tool use. *PeerJ*, 6, e4366. <https://doi.org/10.7717/peerj.4366>
- Haslam, M. (2013). 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1630), 20120421. <https://doi.org/10.1098/rstb.2012.0421>
- Haun, D. B. M., Rekers, Y., & Tomasello, M. (2012). Majority-biased transmission in chimpanzees and human children, but not orangutans. *Current Biology: CB*, 22(8), 727–731. <https://doi.org/10.1016/j.cub.2012.03.006>
- Haun, D. B. M., van Leeuwen, E. J. C., & Edelson, M. G. (2013). Majority influence in children and other animals. *Developmental Cognitive Neuroscience*, 3, 61–71. <https://doi.org/10.1016/j.dcn.2012.09.003>
- Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, 69(2), 207–231. <https://doi.org/10.1111/j.1469-185x.1994.tb01506.x>
- Hirata, S., Morimura, N., & Houki, C. (2009). How to crack nuts: Acquisition process in captive chimpanzees (*Pan troglodytes*) observing a model. *Animal Cognition*, 12 Suppl 1, 87–101. <https://doi.org/10.1007/s10071-009-0275-3>
- Hopper, L. M., Kurtycz, L. M., Ross, S. R., & Bonnie, K. E. (2015). Captive chimpanzee foraging in a social setting: A test of problem solving, flexibility, and spatial discounting. *PeerJ*, 3, e833. <https://doi.org/10.7717/peerj.833>
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2008). Observational learning in chimpanzees and children studied through 'ghost' conditions. *Proceedings of the Royal Society B: Biological Sciences*, 275(1636), 835–840. <https://doi.org/10.1098/rspb.2007.1542>
- Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour*, 81(6), 1195–1202. <https://doi.org/10.1016/j.anbehav.2011.03.002>
- Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & Waal, F. B. M. de. (2010). Prestige Affects Cultural Learning in Chimpanzees. *PLOS ONE*, 5(5), e10625. <https://doi.org/10.1371/journal.pone.0010625>
- Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, 8(3), 164–181. <https://doi.org/10.1007/s10071-004-0239-6>
- Hrubesch, C., Preuschoft, S., & van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Animal Cognition*, 12(2), 209–216. <https://doi.org/10.1007/s10071-008-0183-y>
- Jaeggi, A. V., Dunkel, L. P., Van Noordwijk, M. A., Wich, S. A., Sura, A. A. L., & Van Schaik, C. P. (2010). Social learning of diet and foraging skills by wild immature Bornean orangutans: Implications for culture. *American Journal of Primatology*, 72(1), 62–71. <https://doi.org/10.1002/ajp.20752>

- Jaeggi, A. V., van Noordwijk, M. A., & van Schaik, C. P. (2008). Begging for information: Mother-offspring food sharing among wild Bornean orangutans. *American Journal of Primatology*, 70(6), 533–541. <https://doi.org/10.1002/ajp.20525>
- Kaufman, A. B., Butt, A. E., Kaufman, J. C., & Colbert-White, E. N. (2011). Towards a neurobiology of creativity in nonhuman animals. *Journal of Comparative Psychology (Washington, D.C.: 1983)*, 125(3), 255–272. <https://doi.org/10.1037/a0023147>
- Kaufman, J. C., & Kaufman, A. B. (2004). Applying a creativity framework to animal cognition. *New Ideas in Psychology*, 22(2), 143–155. <https://doi.org/10.1016/j.newideapsych.2004.09.006>
- Kendal, R., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: Implications for cultural diversity. *Evolution and Human Behavior*, 36(1), 65–72. <https://doi.org/10.1016/j.evolhumbehav.2014.09.002>
- Kendal, R. L., Boogert, N. J., Rendell, L., Laland, K. N., Webster, M., & Jones, P. L. (2018). Social Learning Strategies: Bridge-Building between Fields. *Trends in Cognitive Sciences*, 22(7), 651–665. <https://doi.org/10.1016/j.tics.2018.04.003>
- Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-Offs in the Adaptive Use of Social and Asocial Learning. In *Advances in the Study of Behavior* (Vol. 35, pp. 333–379). Academic Press. [https://doi.org/10.1016/S0065-3454\(05\)35008-X](https://doi.org/10.1016/S0065-3454(05)35008-X)
- Kendal, R. L., Custance, D. M., Kendal, J. R., Vale, G., Stoinski, T. S., Rakotomalala, N. L., & Rasamimanana, H. (2010). Evidence for social learning in wild lemurs (*Lemur catta*). *Learning & Behavior*, 38(3), 220–234. <https://doi.org/10.3758/LB.38.3.220>
- Krützen, M., Willems, E. P., & van Schaik, C. P. (2011). Culture and geographic variation in orangutan behavior. *Current Biology: CB*, 21(21), 1808–1812. <https://doi.org/10.1016/j.cub.2011.09.017>
- Kummer, H., & Goodall, J. (1985). Conditions of Innovative Behaviour in Primates. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 308(1135), 203–214.
- Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, 32(1), 4–14. <https://doi.org/10.3758/BF03196002>
- Laland, K. N., & Galef, B. G. (2009). *The Question of Animal Culture*. Harvard University Press.
- Laland, K. N., & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, 9(5), 493–499. <https://doi.org/10.1093/beheco/9.5.493>
- Lehner, S. R., Burkart, J. M., & Schaik, C. P. van. (2011). Can captive orangutans (*Pongo pygmaeus abelii*) be coaxed into cumulative build-up of techniques? *Journal of Comparative Psychology (Washington, D.C.: 1983)*, 125(4), 446–455. <https://doi.org/10.1037/a0024413>
- Lonsdorf, E. V., Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, 428(6984), Article 6984. <https://doi.org/10.1038/428715a>
- Luncz, L. V., Mundry, R., & Boesch, C. (2012). Evidence for Cultural Differences between Neighboring Chimpanzee Communities. *Current Biology*, 22(10), 922–926. <https://doi.org/10.1016/j.cub.2012.03.031>
- Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G. (2001). Emergence of Culture in Wild Chimpanzees: Education by Master-Apprenticeship. In T. Matsuzawa (Ed.), *Primate Origins of Human Cognition and Behavior* (pp. 557–574). Springer Japan. https://doi.org/10.1007/978-4-431-09423-4_28
- McGrew, W., & Tutin, C. (1978). Evidence for a Social Custom in Wild Chimpanzees? *Man*, 13, 234–251. <https://doi.org/10.2307/2800247>

- Mesoudi, A., & Thornton, A. (2018). What is cumulative cultural evolution? *Proceedings of the Royal Society B: Biological Sciences*, 285(1880), 20180712. <https://doi.org/10.1098/rspb.2018.0712>
- Mettke-Hofmann, C., Winkler, H., & Leisler, B. (2002). The Significance of Ecological Factors for Exploration and Neophobia in Parrots. *Ethology*, v.108, 249-272 (2002), 108. <https://doi.org/10.1046/j.1439-0310.2002.00773.x>
- Motes-Rodrigo, A., & Tennie, C. (2022). Captive great apes tend to innovate simple tool behaviors quickly. *American Journal of Primatology*, 84(10), e23311. <https://doi.org/10.1002/ajp.23311>
- Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., & Sanz, C. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports*, 6(1), Article 1. <https://doi.org/10.1038/srep34783>
- Nishida, T., Matsusaka, T., & McGrew, W. C. (2009). Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: A review. *Primates; Journal of Primatology*, 50(1), 23–36. <https://doi.org/10.1007/s10329-008-0109-y>
- Pradhan, G. R., Tennie, C., & van Schaik, C. P. (2012). Social organization and the evolution of cumulative technology in apes and hominins. *Journal of Human Evolution*, 63(1), 180–190. <https://doi.org/10.1016/j.jhevol.2012.04.008>
- Reader, S., & Laland, K. (2003). Animal Innovation: An Introduction. *Animal Innovation*. <https://doi.org/10.1093/acprof:oso/9780198526223.003.0001>
- Rössler, T., Mioduszevska, B., O'Hara, M., Huber, L., Prawiradilaga, D. M., & Auersperg, A. M. I. (2020). Using an Innovation Arena to compare wild-caught and laboratory Goffin's cockatoos. *Scientific Reports*, 10(1), Article 1. <https://doi.org/10.1038/s41598-020-65223-6>
- Russell, P. A. (1973). Relationships between exploratory behaviour and fear: A review. *British Journal of Psychology (London, England: 1953)*, 64(3), 417–433. <https://doi.org/10.1111/j.2044-8295.1973.tb01369.x>
- Sabbatini, G., Stammati, M., Tavares, M. C. H., & Visalberghi, E. (2007). Response toward novel stimuli in a group of tufted capuchins (*Cebus libidinosus*) in Brasília National Park, Brazil. *American Journal of Primatology*, 69(4), 457–470. <https://doi.org/10.1002/ajp.20365>
- Samuni, L., Mundry, R., Terkel, J., Zuberbühler, K., & Hobaiter, C. (2014). Socially learned habituation to human observers in wild chimpanzees. *Animal Cognition*, 17(4), 997–1005. <https://doi.org/10.1007/s10071-014-0731-6>
- Sanz, C. M., & Morgan, D. B. (2007). Chimpanzee tool technology in the Goulougo Triangle, Republic of Congo. *Journal of Human Evolution*, 52(4), 420–433. <https://doi.org/10.1016/j.jhevol.2006.11.001>
- Schuppli, C., Forss, S. I. F., Meulman, E. J. M., Zweifel, N., Lee, K. C., Rukmana, E., Vogel, E. R., van Noordwijk, M. A., & van Schaik, C. P. (2016). Development of foraging skills in two orangutan populations: Needing to learn or needing to grow? *Frontiers in Zoology*, 13(1), 43. <https://doi.org/10.1186/s12983-016-0178-5>
- Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior: The use and manufacture of tools by animals, Rev. and updated ed* (pp. xvi, 282). Johns Hopkins University Press.
- Singleton, I., Knott, C. D., Morrogh-Bernard, H. C., Wich, S. A., & van Schaik, C. P. (2008). Ranging behavior of orangutan females and social organization. In S. A. Wich, S. S. Utami Atmoko, T. M. Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (p. 0). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199213276.003.0013>

- Stout, D., Rogers, M. J., Jaeggi, A. V., & Semaw, S. (2019). Archaeology and the origins of human cumulative culture: A case study from the earliest Oldowan at Gona, Ethiopia. *Current Anthropology*, *60*(3), 309–340. <https://doi.org/10.1086/703173>
- Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2405–2415. <https://doi.org/10.1098/rstb.2009.0052>
- Tennie, C., Call, J., & Tomasello, M. (2012). Untrained Chimpanzees (*Pan troglodytes schweinfurthii*) Fail to Imitate Novel Actions. *PLOS ONE*, *7*(8), e41548. <https://doi.org/10.1371/journal.pone.0041548>
- Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signaling of chimpanzees? In *“Language” and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 274–311). Cambridge University Press. <https://doi.org/10.1017/CBO9780511665486.012>
- Tomasello, M. (2009). *The question of chimpanzee culture, plus postscript (Chimpanzee Culture, 2009)* (p. 221). Harvard University Press. <https://doi.org/10.1007/BF02692251>
- Tomasello, M., Call, J., Warren, J., Frost, G. T., Carpenter, M., & Nagell, K. (1997). The Ontogeny of Chimpanzee Gestural Signals: A Comparison Across Groups and Generations: *Evolution of Communication*, *1*(2), 223–259. <https://doi.org/10.1075/eoc.1.2.04tom>
- Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool-use by young chimpanzees. *Human Evolution*, *2*(2), 175–183. <https://doi.org/10.1007/BF02436405>
- van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate’s foraging decisions. *Science (New York, N.Y.)*, *340*(6131), 483–485. <https://doi.org/10.1126/science.1232769>
- van de Waal, E., Bshary, R., & Whiten, A. (2014). Wild vervet monkey infants acquire the food-processing variants of their mothers. *Animal Behaviour*, *90*, 41–45. <https://doi.org/10.1016/j.anbehav.2014.01.015>
- van de Waal, E., Renevey, N., Favre, C. M., & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1691), 2105–2111. <https://doi.org/10.1098/rspb.2009.2260>
- van Leeuwen, E. J. C., & Haun, D. B. M. (2013). Conformity in nonhuman primates: Fad or fact? *Evolution and Human Behavior*, *34*(1), 1–7. <https://doi.org/10.1016/j.evolhumbehav.2012.07.005>
- van Schaik, C. P. (2012). Animal Culture: Chimpanzee Conformity? *Current Biology*, *22*(10), R402–R404. <https://doi.org/10.1016/j.cub.2012.04.001>
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S., & Merrill, M. (2003). Orangutan Cultures and the Evolution of Material Culture. *Science*, *299*(5603), 102–105. <https://doi.org/10.1126/science.1078004>
- van Schaik, C. P., Burkart, J., Damerius, L., Forss, S. I. F., Koops, K., van Noordwijk, M. A., & Schuppli, C. (2016). The reluctant innovator: Orangutans and the phylogeny of creativity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1690), 20150183. <https://doi.org/10.1098/rstb.2015.0183>
- Waal, E. van de, Krützen, M., Hula, J., Goudet, J., & Bshary, R. (2012). Similarity in Food Cleaning Techniques within Matrilineages in Wild Vervet Monkeys. *PLOS ONE*, *7*(4), e35694. <https://doi.org/10.1371/journal.pone.0035694>

- Watson, S. K., Botting, J., Whiten, A., & van de Waal, E. (2018). Culture and Selective Social Learning in Wild and Captive Primates. In L. D. Di Paolo, F. Di Vincenzo, & F. De Petrillo (Eds.), *Evolution of Primate Social Cognition* (pp. 211–230). Springer International Publishing.
https://doi.org/10.1007/978-3-319-93776-2_14
- Watson, S. K., Reamer, L. A., Mareno, M. C., Vale, G., Harrison, R. A., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2017). Socially transmitted diffusion of a novel behavior from subordinate chimpanzees. *American Journal of Primatology*, 79(6). <https://doi.org/10.1002/ajp.22642>
- Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature*, 437(7055), Article 7055. <https://doi.org/10.1038/nature04023>
- Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 997–1007.
<https://doi.org/10.1098/rstb.2010.0334>
- Whiten, A. (2017a). A second inheritance system: The extension of biology through culture. *Interface Focus*, 7(5), 20160142. <https://doi.org/10.1098/rsfs.2016.0142>
- Whiten, A. (2017b). Social Learning and Culture in Child and Chimpanzee. *Annual Review of Psychology*, 68, 129–154. <https://doi.org/10.1146/annurev-psych-010416-044108>
- Whiten, A., Caldwell, C. A., & Mesoudi, A. (2016). Cultural diffusion in humans and other animals. *Current Opinion in Psychology*, 8, 15–21. <https://doi.org/10.1016/j.copsyc.2015.09.002>
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399(6737), Article 6737. <https://doi.org/10.1038/21415>
- Whiten, A., Goodall, J., McGrew, W., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C., Wrangham, R., & Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, 138, 1481–1516.
<https://doi.org/10.1163/156853901317367717>
- Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437(7059), Article 7059. <https://doi.org/10.1038/nature04047>
- Whiten, A., Horner, V., Litchfield, C. A., & Marshall-Pescini, S. (2004). How do apes ape? *Animal Learning & Behavior*, 32(1), 36–52. <https://doi.org/10.3758/BF03196005>
- Wich, S. A., Utami-Atmoko, S. S., Setia, T. M., Rijksen, H. D., Schürmann, C., van Hooff, J. A. R. A. M., & van Schaik, C. P. (2004). Life history of wild Sumatran orangutans (*Pongo abelii*). *Journal of Human Evolution*, 47(6), 385–398. <https://doi.org/10.1016/j.jhevol.2004.08.006>
- Wood, L. A., Kendal, R. L., & Flynn, E. G. (2013). Whom do children copy? Model-based biases in social learning. *Developmental Review*, 33(4), 341–356.
<https://doi.org/10.1016/j.dr.2013.08.002>
- Yamamoto, S., Humle, T., & Tanaka, M. (2013). Basis for cumulative cultural evolution in chimpanzees: Social learning of a more efficient tool-use technique. *PLoS One*, 8(1), e55768.
<https://doi.org/10.1371/journal.pone.0055768>