

Psychological Sketches
(The “What If?” Edition)

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Chapter 11

How and Why do Human and Nonhuman Cumulative Cultures Differ?

Jean-Baptiste Leca

That's one small step for [a] man, one giant leap for mankind.

Neil Armstrong: July 21, 1969

Cumulative cultural evolution is what *makes us odd*.

Heyes, 2012, p. 2181

EVEN though a wide range of animal taxa have socially transmitted behavioural traditions, human culture appears unique in that it is cumulative: that is, human cultural traits increase in diversity, complexity, and efficiency over extended periods of time. The question of what determine the differences between animal traditions and human culture—and among them, the process of cumulative cultural evolution—was featured in *Science* magazine's (Anonymous, 2005, p. 99) list of 125 things we don't know but that should drive scientific research, as the answer to this question has major implications for human exceptionalism. After briefly defining culture, I will provide comparative evidence for human and nonhuman cumulative cultures, and present the currently proposed hypotheses to explain the differences in cumulative culture between humans and nonhuman animals.

11.1 Defining Culture from a Cross-Species Comparative Perspective

Depending on whether you are a biologist or a socio-cultural anthropologist, culture can be present in thousands of species or be restricted to humans, respectively. Here, I will adopt a definition of culture that serves the main objective of this review, that is, the comparison of the cultural capabilities of humans and other animals. If culture (also termed “behavioural tradition” by ethologists) is defined as a population-specific behavioural practice, persistent in several group members across generations or at least over a number of years, and dependent on social means for its transmission and maintenance (Perry & Manson, 2003), then culture is certainly not limited to humans. There is increasing evidence for cultural variations in a wide range of behavioural patterns (e.g., interspecific interactions, communication, courtship, display, grooming, object play, social play, feeding habits, food processing techniques, medicinal plant use, and tool use) and across various animal taxa (including fish, birds, rodents, cetaceans, and nonhuman primates; Frigaszy & Perry, 2003).

However, some authors argue that “animal behavioural traditions” and “human culture” should be distinguished and considered analogous rather than homologous on the basis of several major differences: (1) the content of what is transmitted (simple behavioural patterns versus elaborate beliefs, social norms, and technical artefacts), (2) the social learning mechanisms that support them (local enhancement and social facilitation versus imitation and teaching), (3) the stability and durability of the phenomenon (ephemeral animal tradition drifts or fads lasting from only a portion of an individual’s life span up to a few generations versus stable human cultural traits enduring across centuries), and (4) the cumulativeness of the process (no obvious improvement of behavioural patterns showing little if any change over generations versus progressive accumulation of cultural modifications over time leading to increasingly complex behaviours) (Laland & Galef, 2009). Here, I will focus on the latter difference: cumulative culture.

11.2 Comparative Evidence for Human and Nonhuman Cumulative Cultures

11.2.1 What is cumulative culture?

Dean, Vale, Laland, Flynn, and Kendal (2013, p. 287) defined cumulative culture as “the modification, over multiple transmission episodes, of cultural traits (behavioural patterns transmitted through social learning) resulting in an increase in the diversity, complexity and/or efficiency of those traits”. It should be noted that the simple accumulation of multiple behavioural traits (e.g., knowledge of different foods) with no modifications over time, or any incremental changes in complexity or efficiency, does not qualify for cumulative culture.

Cumulative cultural evolution refers to situations in which “the achievements of one pattern of behaviour form the basis for the selection of a modified and better-adapted descendant pattern” (Avital & Jablonka, 2000, p. 94). To illustrate this process, Tomasello (1999, p. 5) used the metaphor of the “ratchet”: “The process of cumulative cultural evolution requires not only creative invention but also, and just as importantly, faithful social transmission that can work as a ratchet to prevent slippage backward—so that the newly invented artifact or practice preserves its new and improved form at least somewhat faithfully until a further modification or improvement comes along.” In other words, cumulative culture involves a ratchet-like effect where a beneficial modification is retained (probably via high-fidelity transmission mechanisms), until it can be improved upon, and results in behaviours or artefacts with cultural histories; that no individual could invent on its own (Tomasello, 1999).

As pointed out by Mesoudi, Whiten, and Laland (2004), cumulative cultural evolution, like biological evolution, encompasses Darwinian processes that include competition, variation, geographical distribution, selection, adaptation, inheritance, accumulation of modifications, changes of function, and convergent evolution.

11.2.2 Cumulative culture in humans

On August 5th 2012, the front cover of the special issue of *Philosophical Transactions of the Royal Society B*—focusing on the evolution of human cognition—featured a picture similar to the one in Figure 11.1. It illustrated the combination of two cumulative cultural artefacts characteristic of two periods of hominin evolution: A 300–500 thousand-year-old hand axe,



Figure 11.1: Two cumulative cultural artefacts of hominin evolution: A Swanscombe hand axe displayed by a smart phone (modified from: <http://news.bbc.co.uk/2/hi/science/nature/5392134.stm>)

found at the Swanscombe *Homo neanderthalensis* site, being displayed by another hand-held multipurpose tool of similar size but more recent origin—a so-called “smart phone”. Both artefacts are hallmarks of human exceptionalism.

On July 21st 1969, the American astronaut Neil Armstrong became the first human to step onto the surface of the Moon, and while doing so, he spoke the famous words: “That’s one small step for [a] man, one giant leap for mankind.” Indeed, this huge achievement for humanity was not planned, devised, and executed by Armstrong alone; it was the result of a series of many small and incremental steps involving a team of scientists, technicians, and various stakeholders, combining and deploying a vast range of techniques and technological materials reliant on theoretical and experimental research conducted over several centuries.

As illustrated by these two examples, human societies typically exhibit elaborate cumulative cultural evolution, with new knowledge, methods, and patterns building upon the developments of their predecessors via many episodes of social transmission across generations, often leading to increasing diversity, complexity, and efficiency of cultural or technolog-

ical products which are far beyond what a single individual could have invented alone (Tomasello, 1999; Caldwell & Millen, 2009). The gradual accumulation of such adaptive cultural knowledge, technologies, artefacts, languages, and institutions have played a major role in the remarkable ecological and demographic success of humanity and allowed our species to occupy and exploit a far wider range of habitats than any other animal (Boyd & Richerson, 1996).

On the one hand, there is solid historical evidence for cumulative cultural patterns and products in humans. On an evolutionary time scale, the first signs of cumulative culture are found in the archaeological record of hominin lithic artefacts, (1) starting around 3.4 Mya with the oldest traces of stone tools (i.e., basic stone flakes used by *Australopithecus afarensis* to remove flesh and extract bone marrow from small animals; McPherron et al., 2010), (2) advancing with the appearance of roughly knapped stone tools around 2.6 Mya (i.e., simple chopper, scraper and pounder cores used by *Homo habilis* and characteristic of the Oldowan Industry—or Mode 1 tools), (3) escalating with the emergence of more complex bifaces around 1.8 Mya (i.e., symmetrical and sharp hand axes particularly well-suited to the butchery of large animals, associated with *Homo erectus* or *Homo ergaster*, and characteristic of the Acheulean Industry—or Mode 2 tools), and (4) further improving in Europe around 0.3 Mya with the sophisticated manufacture of a variety of aesthetic tool types from the same stone (including even sharper knife-like, flint, and blade tools associated with *Homo neanderthalensis* and early *Homo sapiens* from 160 kya, and characteristic of the Mousterian Industry—or Mode 3 tools), as well as barbed bone harpoon points (Stout, 2011).

Despite the longevity of the Oldowan and Acheulean Industries and the apparent lack of clear incremental change in over a million years within each of these two periods, recent studies suggest that they should not be regarded as completely static, as they incorporated some geographical and temporal patterning in cultural variants (Stout, 2011). Nevertheless, this relative cultural conservatism (i.e., a very slow rate of improvement and a punctuated—rather than gradual—pattern of Lower Palaeolithic technological change) could be explained in terms of underlying cognitive constraints (i.e., biological—rather than cultural—evolution; Mithen, 1999).

Later signs of rich and accelerating human cumulative culture were found by using multiple historical sources from more recent iconographic and written accounts (from 30,000 BC through the 20th Century) to document, classify and sequence inventions, discoveries, outstanding contribu-

tions, and overall progress in science, technology, and arts, with specific advancement recorded in the fields of physics, chemistry, agriculture, industry, mathematics, medicine, public hygiene, education, architecture, and symphonic music (Lehman, 1947; Basalla, 1988). For example, such historical approach provided evidence for the gradual emergence of complex products or artefacts by ratcheting from simple tally systems to complex mathematical models or early wheels to modern racing cars, satellites and particle accelerators.

On the other hand, experimental research explores the social and cognitive processes underlying such cumulative changes in cultural traits. In the laboratory, diffusion chain experiments are designed by using artificial “generations” of participants (or micro-populations) taking part in a task in series. The first participant acts as demonstrator to the second participant, who will in turn act as demonstrator to the third participant, and so forth. Examples of tasks involve: (1) solving a puzzle box in which access to a reward is made difficult by a series of defences, (2) making a paper aeroplane which should fly as far as possible, and (3) using uncooked spaghetti and modelling clay to build a tower which should be as tall as possible (Mesoudi & Whiten, 2008).

A first line of empirical research aims to test the ratchet hypothesis which holds that cumulative culture depends on the strategic combination of innovation and imitation. Individuals must occasionally invent novel solutions which build upon existing methods, and these modifications must be faithfully transmitted in order to be maintained within the population until they can be further improved. Therefore, researchers compare different experimental conditions in which imitating the demonstrator or coming up with an independent alternative solution to the task are associated with different cost-benefit ratios. Results show strategic shifts between imitation and innovation, depending on whether copying others is experimentally made more effective or counterproductive, respectively. When imitation is made costly or risky, or when it is theoretically possible to perform considerably better than the demonstrator, lower fidelity copying and higher innovation rates are observed. In the absence of any information about the relative effectiveness of alternative methods (i.e., when the payoffs for individually learned behaviors are uncertain), imitation tends to be regarded as less risky than innovation (Caldwell & Millen, 2008; Flynn, 2008).

A second line of empirical research aims to assess which social learning mechanisms can sustain cumulative culture in humans. Here, researchers compare different experimental conditions in which inter-generational

transmission of information is underlain by different mechanisms, such as (1) observing a demonstrator make a paper aeroplane in a certain way and then replicating the exact same sequence of actions (i.e., imitation or process-oriented copying), (2) only witnessing the physical effects of the final product—how far planes made by others can fly—and trying to achieve the same goal (i.e., emulation or product-oriented copying), and (3) benefiting from the active and costly investment by a tutor who can infer the current knowledge state of the pupil and adjust the amount and type of support through directed verbal instruction and/or demonstration of specific steps of the plane construction (i.e., teaching). Results show that any one of these social learning mechanisms is sufficient to elicit a cumulative improvement over the course of the experiments (Caldwell & Millen, 2009). However, it is possible that only higher-fidelity transmission processes (i.e., imitation and teaching) can explain the accumulation of more complex technologies.

11.2.3 Cumulative culture in nonhuman animals?

In striking contrast with the overwhelming evidence and capacity for human cumulative culture, examples of possibly ratcheted behavioural traditions in nonhuman animals are, at best, rare, relatively simple, and limited to a few species. A close look at the literature shows that the very existence of nonhuman cumulative culture is even controversial (Laland & Galef, 2009). However, for comparative purposes, here is a brief overview of the few documented cases in which cultural changes in free-ranging animals seem to accumulate over generations, leading to geographic variation in a wide array of socially transmitted behavioural patterns. This behavioural diversity and complexity is apparently unrelated to local ecological conditions, and in some cases, might be beyond what a single individual could invent alone. In general, such evidence for cumulative cultural transmission in animals comes from long-term observational field studies.

New Caledonian crows manufacture and use different types of tools to extract caterpillars from crevices. With their beaks, these birds cut and rip strips from the barbed edges of *Pandanus* leaves, which make effective hooking-tools. The leaves are cut to three main designs: those designs are uniformly/unstepped wide, uniformly/unstepped narrow, and stepped/tapered tools. Among the stepped tools, the designs further vary from single-stepped shapes to four-stepped shapes, the latter providing a thick/stiff holding end and a thin/flexible probing end, making the tool even more effective. These socially learned variants in tool shapes form a

graded series (from simple unstepped to complex four-stepped tools) with a geographically patchy distribution across New Caledonia that does not seem related to obvious ecological correlates. Moreover, local tool designs can remain unchanged for decades, which is suggestive of a high-fidelity transmission process (Hunt & Gray, 2003).

In some killer whale pods ranging around the Crozet archipelago, the foraging techniques—consisting of briefly beaching in order to prey on elephant seal pups—appear to increase in diversity, complexity, and effectiveness across generations. It has been argued that “social beaching play” among juvenile killer whales may have evolved into “intentional stranding hunting techniques” in adults. The development of these foraging skills could be guided by teaching-like abilities, with adult females assisting their offspring in returning to the water after voluntarily beaching. Such an inter-generational transmission of competence would, in turn, increase the long-term hunting success of the pod (Guinet & Bouvier, 1995).

In Costa Rican white-faced capuchins, there are intergroup differences in social conventions: that is, arbitrary and ritualized dyadic communicative gestures that may function to increase inter-individual tolerance and test social bonds. Such greeting interactions are socially transmitted among group members and take different forms, such as “hand-sniffing” (inserting one’s fingers in or on the nostrils of the partner, often mutually, and for extended periods of time), “sucking/biting on others’ body parts” (e.g., finger-in-mouth game, hair-in-mouth game), and “eye-poking” (inserting the partner’s finger into one’s own eye socket up to the first knuckle). Apparently, these group-specific social conventions emerged in succession with the latter two being modifications of the first (Perry et al., 2003).

Since the Japanese macaques living on Koshima island (southern Japan) have been provisioned with food by local researchers in the early 1950s, this group has gradually acquired a whole new life style. Feeding the monkeys first with sweet potatoes, then with wheat grains, on the sandy seashore, directly led to the appearance of two successive food-washing traditions: (1) “potato-washing”, with an original form described as dipping the potatoes into the freshwater of a nearby stream, thus washing off sand and dirt before eating them, and a subsequent elaboration of this behaviour consisting of biting the potatoes before dipping them into the shallow salty seawater, not only to wash them, but also presumably to season them before they were consumed, and (2) “wheat-washing”, defined as picking up a handful of mixed sand and wheat and throwing it into the seawater, which resulted in separating the heavier sand that sank from the lighter wheat that floated on the surface, allowing the monkeys to collect it

easily (Avital & Jablonka, 2000).

Moreover, the habit of spending more and more time on the beach, an unnatural habitat for Japanese macaques, also had ulterior indirect effects on the diffusion of additional behavioural innovations, through the influence of food provisioning on the troop's activity budget and sedentary lifestyle. As young monkeys brought to the beach by their mothers (who had learned washing their food) became accustomed to the salty water, they started playing in it. Thus, sea-related subsistence traditions triggered the social traditions of using the sea for swimming, jumping and diving, as well as cooling in summer—newly acquired behaviours that became characteristic of the whole troop, including the adults, and had not been reported before in this troop or in other troops of Japanese macaques. Another consequence of these beach activities occurred later: the monkeys started to eat raw fish, a feeding habit that is still present in the troop today (Leca, Gunst, Watanabe, & Huffman, 2007). In sum, Koshima macaques have accumulated and elaborated over decades their food-related and social traditions in a ratcheted way by developing a new lifestyle associated with a new habitat, the sandy beach and the sea.

In another group of Japanese macaques living in the mountains around Kyoto city (central Japan), the monkeys exhibit another behavioural tradition called “stone handling”, a form of solitary but socially transmitted object play which consists of the non-instrumental manipulation of stones by performing various behavioural patterns (e.g., repeatedly pounding a stone on a substrate, clacking two stones together, or gathering several stones into a pile). Three decades of continued observation of this group showed that the monkeys have gradually increased the size and the complexity of their stone handling repertoire and largely diversified the contexts in which stone handling activity is practiced compared to earlier generations of stone handlers (see Figure 11.2). Over time, the accumulation and transformation of stone-directed behavioural patterns could result in the future use of stone as tools (Leca, Gunst, & Huffman, 2012).

Finally, some forms of insect-fishing and nut-cracking behaviours currently performed by particular chimpanzee communities indicate a step-by-step elaboration on earlier and simpler variants that may reflect accumulated modifications of socially transmitted behavioural patterns. In the Goualougo Triangle, Republic of Congo, chimpanzees prepare a termite-foraging tool kit, with multiple types of tools that they use in sequence, for different steps of the same foraging activity. For example, they first use the blunt end of a thick puncturing-stick to perforate subterranean termite-nests. Then, they use the thin end of an investigatory probing-twig

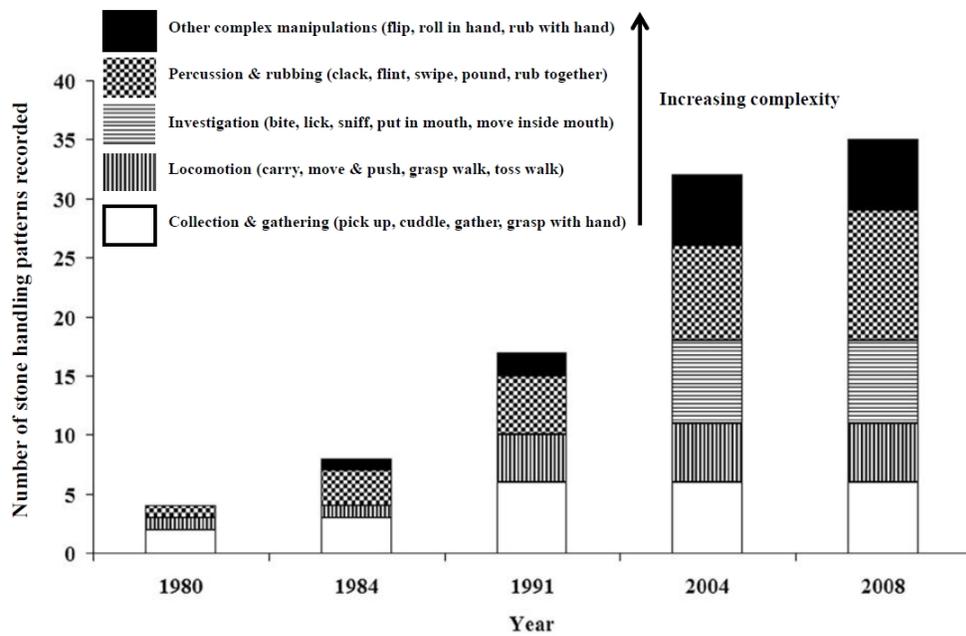


Figure 11.2: Accumulation over time and generations of diversity and complexity in stone handling patterns (modified from Leca et al., 2012)

to explore the inside of the nest. Finally, they make a brush-tipped stick by clenching their teeth onto the tip of a branch and pulling it through their teeth, splitting the end lengthwise into strands. The latter is a particularly effective termite-collector tool. Likewise, the different nut-cracking variants displayed by some populations of chimpanzees across West Africa are believed to be more or less elaborated forms of an ancestral behavioural pattern of hitting nuts on a substrate to smash them (e.g., wooden hammer and wooden anvil, stone hammer and stone anvil, stone hammer and stone anvil with stabilising stone; Boesch, 2003).

Although these observation-based findings are suggestive of some form of ratcheting, many researchers argue that further claim for cumulative culture in nonhuman animals is largely uncorroborated. As they point out, (1) the behavioural modifications over time are small, (2) in most cases, an increase in behavioural diversity and complexity is not clearly accompanied with an increase in behavioural efficiency, (3) there is no direct evidence that the so-called “modified” behavioural patterns are derived from the hypothesized “ancestral” ones, and (4) it is difficult to rule out the possibility that the more complex behavioural variants could have been invented by a single individual anew (Laland & Galef, 2009). Moreover, even though archaeological analyses showed that chimpanzee nut-cracking stone technology could date as far back as 4300 years ago, the level of behavioural modification during that time is still unclear (Mercader et al., 2007).

Recent empirical testing of the capacity for nonhuman cumulative culture used experimental designs similar to those employed in humans (e.g., diffusion chains, imitation-versus-emulation tests), but found little evidence that animals can accumulate modifications to their behaviour. First, most subjects became fixed upon their own particular method to solve a problem and were resistant to learning a new one from conspecifics. Second (and consequently), the performance of the tested subjects was not greatly enhanced after observing a demonstrator trained to use a more efficient method to solve a problem. Third, because some control subjects, who received no demonstration of the so-called “modified and more complex” behavioural patterns, were also able to perform them, questions about whether they were really beyond a single individual’s capabilities arose (Tennie, Call, & Tomasello, 2009).

Taken together, these results suggest that even though there is ample evidence for behavioural innovation and socially transmitted behavioural patterns in nonhumans, leading to a variety of group-specific traditions, “animal cultures are either not cumulative at all or cumulative in a highly

restricted and simple manner” (Dean et al., 2013, p. 292).

11.3 Why Are There Differences in Cumulative Culture between Humans and Nonhuman Animals?

Numerous hypotheses have been proposed to explain the evolution of cumulative culture (or lack thereof). Current evidence supports the view that a package of socio-cognitive capabilities (including imitation, teaching, verbal instruction and prosocial tendencies) present in humans, but absent or present to a lesser extent in other animals, underpins cumulative cultural learning, probably because it promotes high-fidelity information transmission. Indeed, imitation and teaching, facilitated by language, cooperation, and shared motivations of individuals, allow for the strict replication of behavioural patterns performed by skilled group members, and scaffold the learning of naïve individuals by saving them from “reinventing the wheel” when a new behaviour is required (Dean et al., 2013).

Other socio-cognitive hypotheses hold that, compared to humans, non-human animals would have (1) lower abilities to innovate, which may preclude incremental improvement in behavioural performance, (2) higher behavioural conservatism or functional fixedness, which may hinder behavioural changes, (3) weaker conformity-biased learning (defined as the disproportionate likelihood of copying what the majority does), which may lead to lower-fidelity transmission at the group level, (4) weaker selective copying abilities (defined as the disproportionate likelihood of copying what the most successful individuals do) which may prevent behavioural improvements from accumulating, and (5) poorer adaptive filtering mechanisms, which may prevent naïve individuals from evaluating the consequences of observed behaviour. However, research on such cognitive differences between humans and nonhuman animals and their real impact on the evolution of cumulative culture has produced equivocal results (Dean et al., 2013).

In addition to socio-cognitive explanations, socio-demographic factors (including the social structure, size, and mobility of populations) can affect the speed of behavioural ratcheting and the maintenance of behavioural diversity (Pradhan, Tennie, & Schaik, 2012). Arguably, increased sociability (i.e., higher inter-individual tolerance, lower dominance gradient, and lack of resource monopolization) enhances behavioural coordination in space and time, which facilitates high-fidelity social learning opportunities (i.e., a prerequisite for cumulative culture). Moreover, mathematical models show

that (1) high population densities, with overlapping generations and the opportunity for learning from multiple individuals, promote cumulative cultural transmission, and (2) high intergroup migration rates allows for a continued flow of cultural practices between populations, accentuating the probability that behaviours will accumulate within and across populations. All these socio-demographic factors were present in ancestral human populations during the late Pleistocene and have probably facilitated the emergence of modern human behaviour through cumulative culture (Powell, Shennan, & Thomas, 2010).

In conclusion, although the evidence for cumulative culture in nonhuman animals is limited, circumstantial and strongly contested, it should be remembered that absence of evidence is not evidence of absence. There might be simpler explanations, such as the lack of research on the topic or the paucity of long-term field studies, which would allow researchers to witness a possible accumulation of cultural variants. There is clearly good reason to remain open-minded with regard to the question of whether cumulative cultural evolution is unique to humans.

References

- Anonymous. (2005). So much more to know. *Science*, 309, 78-102.
- Avital, E., & Jablonka, E. (2000). *Animal traditions: Behavioural inheritance in evolution*. Cambridge, UK: Cambridge University Press.
- Basalla, G. (1988). *Evolution of technology*. Cambridge, UK: Cambridge University Press.
- Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology*, 12, 82-91.
- Boyd, R., & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy*, 88, 77-93.
- Caldwell, C., & Millen, A. (2008). Experimental models for testing hypotheses about cumulative cultural evolution. *Evolution and Human Behavior*, 29, 165-171.
- Caldwell, C., & Millen, A. (2009). Social learning mechanism and cumulative cultural evolution. *Psychological Science*, 20, 1478-1487.
- Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2013). Human cumulative culture: A comparative perspective. *Biological Reviews*, 89, 284-301.
- Flynn, E. (2008). Investigating children as cultural magnets: Do young children transmit redundant information along diffusion chains?

- Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3541-3551.
- Fragaszy, D. M., & Perry, S. (2003). *The biology of traditions: Models and evidence*. Cambridge, UK: Cambridge University Press.
- Guinet, C., & Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology*, 73, 27-33.
- Heyes, C. (2012). Grist and mills: On the cultural origins of cultural learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2181-2191.
- Hunt, G. R., & Gray, R. D. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society B: Biological Sciences*, 270, 867-874.
- Laland, K. N., & Galef, B. G. (2009). *The question of animal culture*. Cambridge, UK: Cambridge University Press.
- Leca, J.-B., Gunst, N., & Huffman, M. A. (2012). Thirty years of stone handling tradition in Arashiyama-Kyoto macaques: Implications for cumulative culture and tool use in non-human primates. In J.-B. Leca, M. Huffman, & P. L. Vasey (Eds.), *The monkeys of stormy mountain: 60 years of primatological research on the Japanese macaques of Arashiyama* (p. 223-257). Cambridge, UK: Cambridge University Press.
- Leca, J.-B., Gunst, N., Watanabe, K., & Huffman, M. A. (2007). A new case of fish-eating in Japanese macaques: Implications for social constraints on the diffusion of feeding innovation. *American Journal of Primatology*, 69, 821-828.
- Lehman, H. C. (1947). The exponential increase in man's cultural output. *Social Forces*, 25, 281-290.
- McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., ... Bearat, H. A. (2010). Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, 466, 857-860.
- Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., & Boesch, C. (2007). 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Science*, 104, 3043-3048.
- Mesoudi, A., & Whiten, A. (2008). The multiple roles of cultural transmission experiments in understanding human cultural evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3489-3501.

- Mesoudi, A., Whiten, A., & Laland, K. N. (2004). Is human cultural evolution Darwinian? *Evolution*, *58*, 1-11.
- Mithen, S. (1999). Imitation and cultural change: A view from the stone age, with specific reference to the manufacture of handaxes. In H. O. Box & K. R. Gibson (Eds.), *Mammalian social learning: Comparative and ecological perspectives* (p. 389-413). Cambridge, UK: Cambridge University Press.
- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., McKinnon, K. C., ... Rose, L. (2003). Social conventions in wild white-faced capuchin monkeys. *Current Anthropology*, *44*, 241-268.
- Perry, S., & Manson, J. H. (2003). Traditions in monkeys. *Evolutionary Anthropology*, *12*, 71-81.
- Powell, A., Shennan, S. J., & Thomas, M. G. (2010). Demography and variation in the accumulation of culturally inherited skills. In M. J. O'Brien & S. J. Shennan (Eds.), *Innovation in cultural systems: contributions from evolutionary anthropology* (p. 137-160). London, UK: MIT Press.
- Pradhan, G. R., Tennie, C., & Schaik, C. P. van. (2012). Social organization and the evolution of cumulative technology in apes and hominins. *Journal of Human Evolution*, *63*, 180-190.
- Stout, D. (2011). Stone tool-making and the evolution of human culture and cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 1050-1059.
- 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*, 2405 - 2415.
- Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.