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Review

Blind alleys and fruitful pathways in the comparative study of cultural cognition

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Abstract

A mere few decades ago, culture was thought a unique human attribute. Evidence to the contrary accumulated through the latter part of the twentieth century and has exploded in the present one, demonstrating the transmission of traditions through social learning across all principal vertebrate taxa and even invertebrates, notably insects. The scope of human culture is nevertheless highly distinctive. What makes our cultural capacities and their cognitive underpinnings so different? In this article I argue that in behavioural scientists' endeavours to answer this question, fruitful research pathways and their ensuing discoveries have come to exist alongside popular, yet in the light of current empirical evidence, highly questionable scenarios and even scientific blind alleys. I particularly re-evaluate theories that rely on the centrality of a supposed uniquely human capacity for imitative copying in explaining the distinctive capacity for massive cumulative cultural evolution (CCE) in our species. The most extreme versions of this perspective suffer logical incoherence and severe limits on scientific testability. By contrast the field has generated a range of rigorous observational and experimental methodologies that have revealed both long-term cultural fidelity and limited forms of CCE in non-human species. Attention now turns to directly investigating the scope, limits and underlying cognition of non-human versus human CCE, with a broader approach to factors additional to cultural transmission, notably the role of invention, innovation and evolved motivational biases underlying the scope of CCE in the species studied.

Keywords: Culture; Cumulative culture; Cultural evolution; Imitation; Ratchet effect; Zone of latent solutions

1. Introduction

Mere decades ago, culture was assumed a unique attribute of humanity. The Nobel Prize winning biologist, Sir Peter Medawar, wrote that "Human beings owe their biological supremacy to a form of inheritance quite unlike that of other animals: exogenetic or exosomatic inheritance. In this form of heredity information is transmitted from one generation to the next generation by non-genetic means .... in general, by the entire apparatus of culture" [1, p. 150]. Remarkable discoveries emerging since have shown that to the contrary, this form of inheritance – the transmission of behaviour across populations and generations through social learning (learning from others) - is widespread among

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animals, as described further below. Such revelations offer significant challenges to earlier conceptions about the distribution of cultural phenomena, in a range of disciplines spanning anthropology, evolutionary biology and the cognitive and behavioural sciences at large [2].

Just three decades ago, Tomasello et al. [3] opened what was to become a highly influential[1] article by concurring with Medawar that “Many animals live in complex social groups; only humans live in cultures” [3, p. 495]. Tomasello et al. then focused more specifically on *cumulative culture*,[2] characterised, they suggested, by a “ratchet effect” in which innovations are faithfully preserved in cultures until further innovations upgrade them, and further cycles of this process repeat. They asserted that “No cultural products exhibiting anything like the ratchet effect have ever been observed in the ontogenetically acquired behaviours or products of nonhuman animals” [3, p. 495]. The authors went on to argue that cumulative culture is supported by three forms of cultural cognition arising sequentially - and uniquely - in human childhood: (a) imitative learning; (b) instructed (taught) learning; and (c) collaborative learning, involving contributions by two or more interacting partners.

Core propositions in this article – notably that (i) cumulative culture is uniquely human; (ii) it depends on uniquely high-fidelity transmission of cultural phenomena to learners; and (iii) that imitative learning is instrumental in this, and also uniquely human - have since become oft-cited ‘conventional wisdoms’ - across a wide diversity of disciplinary literatures.[3] However, research in the ensuing decades has revolutionized our understanding of the scope of both culture per se and of cumulative culture, together with their associated cognitive underpinnings in both humans and nonhuman animals (henceforth ‘animals’). These developments argue that the reappraisal I offer in this article of the propositions outlined above is overdue, especially considering that severely opposing views on ‘the truth of the matter’ concerning animal versus human culture (and cumulative culture and cultural cognition) have multiplied in scientific literatures in recent years. In the following section I present an overview of the principal scientific developments and debates, as context for the detailed reappraisal that follows.

2. Radical transformations and debates in understanding animal versus human culture

2.1. The burgeoning reach of animal culture

The first signs of animal culture were already reported around the middle of the twentieth century, well before the Medawar and Tomasello et al. assertions quoted above. These included such now celebrated cases as the diffusion across the UK of milk-bottle raiding by tits [4], regional birdsong dialects [5] and foraging innovations such as sweet-potato washing in Japanese monkeys [6]. Numerous other well-documented examples in mammalian, avian and

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[1] Citations exceeding 3,200 in Google Scholar and 1,100 in Web of Science.

[2] A number of variations in the terminologies and conceptualizations of cumulative culture have arisen in the literature, being treated as synonyms by some authors but distinguished by others. Variations include *cultural evolution*, *cumulative culture* and *cumulative cultural evolution* (CCE). Potential distinctions between these are not straightforward: in one sense all evolution is cumulative, building on what went before, even where the changes include cetaceans losing limbs or cave dwelling animals losing their vision. Mesoudi and Thornton [63] usefully synthesise the approach of many authors to *cumulative culture*, or *cumulative cultural evolution* (CCE) as involving four core criteria: (i) change in behaviour (or some other entity like an artifact); (ii) transmission of it through social learning; (iii) some improvement in performance; and (iv) sequential repetition of this sequence. However *cultural evolution* appears to be applied to some cases where there is cultural change, but not necessarily clear evidence of criterion (iii); its most common appearance in article titles concern changes over time in birdsong [36] (however see Williams and Lachlan [43] for evidence that criterion (iii) is met in some instances). Accordingly Whiten [36] offered a hierarchical classification in which subcategories of *cultural evolution* included (i) loss of characters; (ii) change in characters; and (iii) accumulation of characters (*cumulative culture* or CCE). In this article I adopt the acronym of CCE for short.

[3] Illustrative examples include: “Today, the concept of culture boasts several conflicting definitions: (1) socially acquired practices (the weakest of the set and the basis for the nonsense about chimpanzee culture)” [183]; “The key to understanding how humans evolved and why we are so different to other animals is to recognise that we are a cultural species. Probably over a million years ago, members of our evolutionary lineage began learning from each other in such a way that culture became cumulative” [131, p. 3]; “It is widely agreed that, although some species of nonhuman animals have “traditions” – they show local variations in behavior due to social learning – nonhuman animals do not have “culture” as culture is characterised by selectionist theories. Specifically in nonhuman animals, modifications to socially learned characteristics cannot accumulate over time in a way that includes improvement” [184], p. 48; see also [90]; “Distinctively human cognitive mechanisms – such as language, ... imitation . . . – are not “cognitive instincts” (Pinker 1994 [185]) but “cognitive gadgets.” These mechanisms, which are absent or merely nascent in other animals, were not designed by human minds, but they are the products of human rather than genetic agency” [93]. “High fidelity preservation of non-instrumental culture is just as much a hallmark feature of our species as is technological invention through sequential change” [186, p. 2].

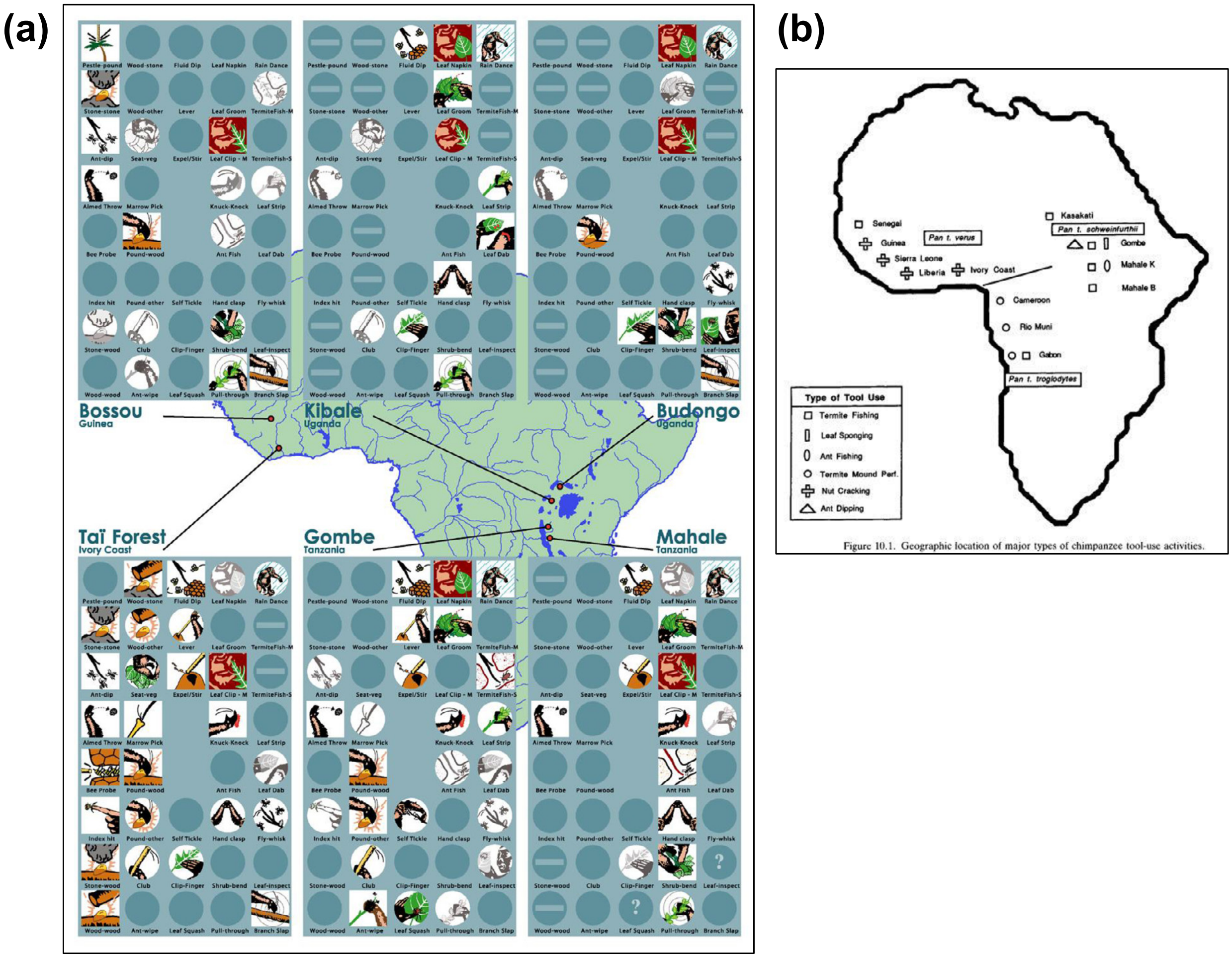

Fig. 1. (a) Distribution of putative cultural variants in chimpanzees across six long-term study sites (after [12]). Squares icons, customary in community; circular icons, habitual (seen repeatedly in multiple individuals); greyed icons, present but not habitual; clear, absent; horizontal bar, absent with inferred ecological explanation; question mark, answer uncertain. 'Cultural variants' are defined as behaviour patterns common (customary or habitual) in at least one community yet absent without apparent ecological explanation in at least one other. Behaviours are arranged in the 5 × 8 arrays to cluster those behaviours as customary or habitual at each site, with clusters for westerly sites on the left of the array and clusters for easterly sites on the right. (b) A contrasting earlier picture of the scope of chimpanzee culture as portrayed by Tomasello [14].

piscine species accumulated through the remainder of the century [2,7, for reviews], bolstered by the development of rigorous experimental techniques to trace social transmission across populations [e.g. [8]; [9], for a review].

Long-term field studies of apes, particularly chimpanzees, increasingly pointed to the existence not merely of single traditions like those noted above, but of complex cultures composed of numerous different traditions, the pattern manifest in our own species [10,11]. By the turn of the century, systematic syntheses of these discoveries identified local chimpanzee cultures differentiated by arrays of traditions spanning much of the species' behavioural repertoire, from tool use and other foraging skills to social, sexual and communicative customs [[12,13]; Fig. 1a]. This picture contrasted markedly with Tomasello's portrayal of just a decade earlier [[14]: Fig. 1b] and has since been further extended [15]. Similar complexities were later identified in other apes [16,17] and monkeys [18,19], as well as the first explorations of such phenomena in cetaceans [20].

Research on animal culture has further flourished in the present century, benefitting from the fruition of long-term field studies and a diversity of methodological advances including new experimental and statistical techniques used to track cultural transmission as innovations diffuse across and between populations [21]. Cultural transmission has been documented in all principal groups of vertebrate, as well as invertebrates, notably insects, and has been discovered to span virtually all major domains of animal behaviour [2,22, for reviews]. In relation to questions about the evolution of cumulative culture, the expanding range and scope of recent discoveries is important to fully acknowledge, because their wide distribution across species and behavioural domains imply extensive reservoirs of potential for cumulative evolutionary change – the topic of section 2.2 below.

Because transmission necessitates the demonstration of a causal role for social learning, experimental manipulations have been particularly valuable in this research. Those conducted in the field offer optimal ecological validity. For example van de Waal et al. [23] used a distasteful additive to train different groups of vervet monkeys to prefer just one of two colours of provisioned corn. In later tests without any additive 27/27 infants naïve to the corn adopted the colour consumed by their mothers, and 9/10 immigrant adult males dispersing from a group that ate one colour, quickly switched to the other colour that was the norm in their new group. Aplin et al. [24] similarly applied this "two-option" experimental approach, training a small number of great tits to push just one of two opposite sides of a foraging device. Each option spread in the community into which it was introduced, as naïve birds increasingly conformed to the local variant, with strong fidelity of transmission into a second year. Mueller et al. [25] imprinted crane chicks on microlight aircraft, thence showing that these surrogate parents could lead fledged individuals over flight paths that were then adopted in later years. In a further experimental variant, cross-fostering via egg-swapping showed that great tits and blue tits would inherit, via social learning, aspects of their foster parents' style of foraging, such as foraging height in the canopy and prey size [26].

Experimental studies of cultural transmission in captive populations are complementary to such field experiments and can often engineer finer-scaled control conditions. Of 33 cultural diffusion experiments published 1972-2008 [27], 30 were with captive populations. Whiten et al. [9] were able to review a further 30, by which time half were field experiments like those reviewed above. The earlier tranches of captive experiments pioneered three complementary designs: *transmission chains* in which each potential social learner became the model witnessed by the next subject in the chain, A-B-C etc.; *replacement chains* in which experienced individuals were replaced stepwise with naïve individuals who can learn from the remaining residents, ABC-BCD-CDE-DEF; and *open diffusion* in which models were introduced into whole groups. The most illuminating designs introduce alternative action sequences into different groups. Some additionally employed baseline control observations at the outset, or parallel controls with no model, to determine the probability of spontaneous performance of the actions introduced. This diversity of methodological approaches delivered positive evidence of cultural transmission across primates, rodents, birds, fish and insects, although a few studies found either no transmission or that differences between incipient alternative traditions faded after a few generations [9].

To illustrate the diversity of these 'diffusion' studies I here outline three. Menzel et al. [28] pioneered a replacement design, in which three juvenile chimpanzees were first exposed to alarming novel objects that elicited avoidance, then one individual was replaced by a naïve one. Repetitions of this process meant that later trios included no individuals from three steps earlier. Nevertheless, over time avoidance lessened and the later trios interacted with the objects. This meant reduced avoidance was socially transmitted, generating cumulative habituation [29]. Such approaches recently extended to insects. Alem et al. [30] reported that bumble-bees learned by observation of a trained model to pull string attached to an artificial flower under a cover, so gaining a reward, a technique not discovered in hives with no model. The technique spread to others in each model's hive, extending to transmission along a chain of as many as four consecutive learners. Danchin et al. [31] likewise employed transmission chains, in which six female fruitflies watched the preferences of other females who preferred to mate with either pink or green dusted males and then in turn became the models for a further set of females to observe. Preferences persisted across eight such "cultural generations".

In the wild, such experimental control is often not possible, but natural experiments occur when ethologists witness spontaneous innovations, and sophisticated statistical techniques have then tracked their spread. For example the performance of a novel addition to their fish-capture techniques by humpback whales was first observed in just one or two individuals but over 26 years spread to over 600 other whales. Network based diffusion analyses (NBDA) revealed that the behaviour spread across social networks, implicating cultural transmission [21]. Similarly, a novel version of tool use, making natural sponges from moss instead of leaves, spread along social network lines in chimpanzees, implicating social transmission [32]. In another example, a chimpanzee in one of four African sanctuary enclosures began leaving a grass leaf in one ear, an "arbitrary" action that then spread to most of her group, but never occurred in the other three enclosures and has not been reported in other chimpanzees [33].

Opportunities to record and track such occurrences are rare, but culture has been inferred through contrasts between neighbouring communities that share similar habitats and genetic exchange, negating ecological and genetic explanations. For example Samuni et al. [34] reported that each of two bonobo communities showed strong preferences to hunt different prey species within the same very large overlap area between their home ranges. Luncz and Boesch [35] showed that neighbouring communities of chimpanzees displayed different patterns of tool-aided nut-cracking, despite migration of sexually maturing females between the commmunities.

2.2. The further discovery of cultural evolution and cumulative culture in animals

The burgeoning reach of animal culture has been progressively uncovered over approximately the last seven decades, but in recent years evidence for cumulative cultural evolution (CCE[2]) has additionally begun to be reported [29,36–38]. The most recent review lists 26 candidate exemplars that span 13 species of mammals, birds and insects [39]. Although the earliest claims for CCE were focused on chimpanzee technologies [40], linking with the focus on technology as a core component of human stone age CCE, recent animal candidates have extended to quite different behavioural domains, including navigational skill in homing [41], seasonal migratory skill [42], and vocal repertoires in birds [43] and whales [44]. Although the differences between any of these cases and the enormous scope of human CCE are vast, their existence and diverse natures provide further justification for a reappraisal of the dominant explanations in the literature for the emergence of cultural evolution and cumulative culture.

2.3. Theoretical entrenchments: “ratcheting up the ratchet”

While the discoveries outlined above have been interpreted by many as helping to illuminate what does and does not distinguish animal and human cultural phenomena [45–48], long-standing debates about this, glossed as “Chimpanzee Culture Wars” because of an overriding focus on our closest relatives [49] have become more entrenched in some quarters. In “Ratcheting up the ratchet”, Tennie, Call and Tomasello [50] gave their view a sharper edge, arguing that lack of imitative copying in apes (and by implication, all animals), limits their cultures to a ‘zone of latent solutions’ (ZLS), conceptualized as the actions latent within them that members of the species can achieve through their own efforts, given sufficient time - “within their lifetime” if necessary [51, p. 430]. It was argued that “only humans could copy traits beyond their ZLS” [51, p. 430], so making cumulative culture possible, with apes and other species being constrained to socially learning only those behaviours within their ZLS. Tennie and colleagues subsequently embarked on an experimental program interpreted as supporting this hypothesis.

These entrenchments provide a further significant justification for a timely reappraisal of the debates alluded to above. I begin by addressing head-on the more recent ZLS hypothesis specifically, together with its core empirical studies. I list five principal weaknesses that together suggest the ZLS hypothesis, as formulated, represents a sterile pathway in our efforts to understand cultural evolution. I then take issue with the broader view widespread since [3] that imitation [50], or more broadly, copying the form of actions new to the learner [51,52], is a unique human capacity. I then turn to more fruitful interpretations and approaches to understanding the nature and evolution of culture in human and non-human animals in Sections 5–7. I must focus on chimpanzees frequently because the extent of research efforts, and key debates, have been the most intense concerning chimpanzee-human contrasts. More research has been conducted on social learning and cultural transmission in chimpanzees than any other species. Where appropriate I include research on a greater diversity of species.

3. The zone of latent solutions concept: sense or nonsense?

I first highlight two fundamental logical problems in the ZLS hypothesis and a further three problems in associated empirical research.

3.1. Logical incoherence

The core of the ZLS hypothesis states that chimpanzees and other apes (and likely other non-human animals) are unable to copy innovations in know-how beyond their ZLS, and so are incapable of exhibiting cumulative culture that incorporates such innovations [50–52]. There is a logical incoherence in this that makes it impossible to test and potentially empirically refute in a biologically meaningful way. If chimpanzees (for example) by definition cannot achieve an innovation beyond their ZLS, how could whether or not others can copy such an advance from them ever be tested? If one or a few chimpanzees create an innovation beyond what scientists believed the species' ZLS in some domain to be, then the ZLS attributed to chimpanzees must expand to include this. This makes the ZLS hypothesis no more than a circular and self-fulfilling prophecy. If by definition a species cannot exceed its ZLS to create an innovation that allows the ZLS hypothesis about inability of others to copy it to be tested, it is fundamentally illogical as a testable and refutable scientific hypothesis: a blind alley. Although we can test whether a non-human species can acquire by observation novel, *human-contrived* challenges that they cannot achieve independently (e.g. see evidence for this in [53]), this obviously does not correspond to the biologically meaningful question of whether a species can, or cannot (as the ZLS hypothesis proposes) copy a new action invented by a conspecific, thwarting its incorporation into cumulative culture. If this analysis is correct, it alone condemns the ZLS as a useful scientific hypothesis.

3.2. All culturally transmitted behaviours require initial individual invention

In some writings, Tennie et al. [51, p. 431] infer that if a single individual achieves a certain behaviour without having seen it in others, that is within the ZLS of the species as a whole. Later [51, p. 438] they suggest that two individuals independently achieving a behaviour is sufficient to imply this. However, all cultural achievements of chimpanzees (or other species) will have begun with an innovator creating the behaviour of interest, rather than learning it from others. Thus it will be no more than a truism that at least one individual has, through its own efforts, been able to perform a behaviour that has since spread to become cultural. The concept of a ZLS provides no additional insight into this state of affairs. Instead it obfuscates it.

Moreover, the inferential leap from finding innovations in 1-2 individuals to ascribing them to the species as a whole is counter to the extensive evidence of intraspecific variation in cognition documented (and not unexpected) in numerous species [54]. It also neglects the fundamental functional significance of social learning, whereby large numbers of conspecifics can benefit by learning from the discoveries of new adaptive actions by others, who sometimes may be just one or two rare, possibly gifted, innovative individuals [55]. Nut-cracking in wild chimpanzees may be a helpful example. Its wide distribution across four contiguous far-western African range states, versus absence from other African regions, is notable. This contrast occurs despite the plentiful availability of raw materials elsewhere [56,57]. Thus nutcracking has become a widely distributed culture, yet is very rarely innovated. One invention by a single chimpanzee long ago (noting archaeological evidence of a duration exceeding 4,000 years [58]) may have sufficed. A single short-term report of nut-cracking in central Africa [59] remains to be confirmed, which a recent survey failed to do [60]. But if one Western Chimpanzee invented nut-cracking, it would be unsurprising if another elsewhere did so at some point in time. This would not mean nutcracking is within the capacity of all or even many other conspecifics to invent. The absence of nutcracking across the other 21 habitat countries for *Pan troglodytes* is evidence to the contrary.

Once, a wild chimpanzee cracked the first nut. Contemplating the implications for the ZLS hypothesis at this time presents a conundrum that highlights points 3.1 and 3.2 above. What would proponents of the ZLS hypothesis need to infer was the ZLS of other chimpanzees at this time, who had never cracked nuts? Or those of the generation before, when no chimpanzee cracked nuts? The same conundrum applies for the first invention of any animal behaviour that is transmitted culturally.

3.3. Inadequate rationale for proposed initial testing

The experimental approach first applied by Tennie et al. [50] to supposedly test the ZLS hypothesis is also illogical. In that study a baseline trial of 5 minutes (hardly a lifetime) was first conducted in which great apes of several species were given a wool braid that if looped could be used to rope in a food reward on a horizontal platform. When no ape did this it was classed as beyond their ZLS. When they were shown by a human how to loop the platform in, no apes copied this. The authors erroneously concluded this was support for their ZLS hypothesis. In the same journal issue, following editorial exchange of pre-publication manuscripts, Whiten et al. [61] noted that this conclusion was unwarranted because the looping manoeuvre may simply be beyond the tested animals' capabilities. By analogy, that apes cannot fly by their own efforts, nor learn it from watching birds fly, is not support for the ZLS hypothesis.

Note also that the loop test presented an 'innovation' created by a different species. But as noted in 3.1, the question of any species' capacity for cumulative culture requires that innovations are generated by a conspecific: whether others can acquire this through social learning can then be evaluated. The fundamental logical incoherence described in 3.1 above is thus here re-emphasised when empirical testing is contemplated.

3.4. Impracticality of testing a "within-ZLS" criterion of "individually achievable within a lifetime"

As several authors have already observed [39,62–66], this criterion is impractical to apply to long-lived species like apes (and unethical if it were to involve rearing as an isolate individual[4]). The "lifetime" criterion also neglects that for apes and other mammals in the wild, many core foraging and other life skills must be learned before weaning [67]. The luxury of individual discovery later in life is thus often not an option. Even if testing is focused on the early juvenile period, the young of both non-human species and human children may already have a cultural repertoire relevant to the skill at stake, so a 'pure' test of a ZLS is unattainable [39].

Presumably the ZLS concept should also apply to humans, but how could the scope of a human ZLS ever be empirically established? It is not obvious that any sensible answers are available, or could realistically be offered.

Of course a shorter period of individual exposure to a task new to an individual can be contrasted with a condition in which subjects can observe a model performing the task, with superior performance in the latter condition thus identifying social learning. But contrasting such conditions is nothing new – it has been a staple experimental approach to identifying social learning for decades (e.g. [68]). Even considering more elaborate experimental designs that test for cultural diffusion along chains or across groups of individual fish, mammals and birds, a review of these [27] identified three studies that included baseline no-model control conditions and eight that included no-model control conditions in parallel with conditions allowing observation of a model. None of these approaches required, nor are newly illuminated by, the concept of a ZLS given the fundamental defects noted above.

3.5. Ecological inadequacy of extant tests for individual invention of traits putatively cultural in the wild

Bandini and Tennie [69,70] have suggested that an alternative test for a ZLS is to discover whether putative cultural behaviours in the wild can be re-invented by captive individuals lacking relevant models to learn from. This makes more sense in principle, but attempted implementations with captive subjects, presented as affirmative cases of such invention, offer inadequate matches to what occurs in the wild. Here I describe such contrasts in five recent examples.

3.5.1. Pestle pounding

Pestle pounding was described as a new type of tool using behaviour in chimpanzees by Yamakoshi and Sugiyama [71]. It involves climbing into the crown of an oil-palm tree, and having plucked out leaf petioles around the central growing point and eaten their soft bases, standing bipedally and repeatedly pounding a large palm frond into the apical growth crown of the tree, creating a juicy pulp in a deepening hole there (Fig. 2a). Repetition creates a cavity sometimes so deep that an arm needs to be inserted up to the shoulder to extract the last pulp. Access by observers on the ground is naturally limited but the authors obtained two discarded tools, one approximately a meter long, the other two meters. Pestle pounding was until recently described only for the Bossou study site in Guinea, but later observed at Kpala in Liberia, about 60 km from Bossou [72]. To date it appears to occur only in this part of West Africa, and not elsewhere, despite the availability of appropriate palm trees [12,13].

Bandini and Tennie [70] reported a study said to "experimentally test the ZLS hypothesis for pestle pounding, a wild chimpanzee behaviour" (p. 1). The authors purported to do this by placing a part-baked potato in a cup with a hole in the top, the cup being attached to the mesh of a participant's cage (Fig. 2b). Chimpanzees could not be tested as individuals, so were tested in four groups. In three of these one individual spontaneously used one of many sticks in their enclosure to probe and pound into the hole, thus extracting some of the potato they could lick off. This did not occur in the fourth group.

Whether the authors created anything like a realistic analogue of oil palm tree pestle pounding in the wild can be judged when Fig. 2b is compared alongside Fig. 2a. In the experimental test the confined chimpanzees were presented

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[4] But isolation in early life has been considered ethical by some in the case of birdsong, from the earliest by Thorpe [187] to Feher et al. [188]. In chaffinches and zebra finches respectively, these studies found that isolate birds fail to develop the 'wild type' song produced by those who learn from conspecifics. Consequently such species of songbirds normally learn by copying songs that are beyond what Tennie and Bandini would call their ZLS. It follows that this phenomenon is far from limited to humans.

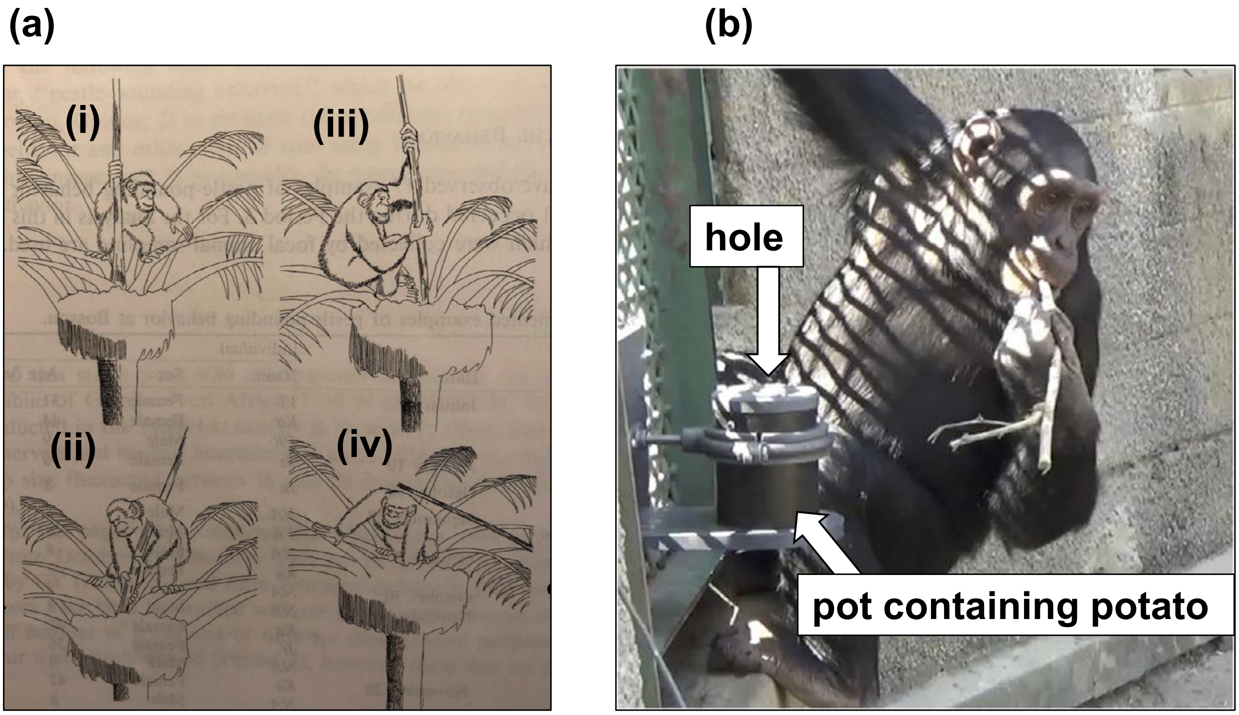

Fig. 2. (a) The sequence of 'pestle-pounding' in wild chimpanzees [71]: chimpanzee (i) spreads mature leaves: (ii) forcefully pulls out shoots round the palm tree crown; (iii) uses a large frond to forcefully pound the crown heart; (iv) reaches in, sometimes to arm's length, to extract pulp. (b) set-up for testing spontaneous pounding in captive chimpanzee, with cup containing part-boiled potato [70]. See text for full descriptions.

with a cup right before them. They had a simple probing opportunity, commonly performed by chimpanzees; smelling the potato, they found a stick and unsurprisingly poked it in the hole. It is more surprising that in one group no chimpanzee did this. In the wild what is needed is far from staring them in the face: invention of the technique required a chimpanzee or chimpanzees to scale a large palm tree and operate on a whole body scale to detach and wield a large palm frond to create the pulp, and extract it by often deep, arm-long reaching.

3.5.2. Algae scooping

Algae scooping by Bossou chimpanzees was first reported in [73]. It involves fashioning a stalk or stick by removing attached foliage, then using this tool to scoop filamentous algae from ponds of water, using a "gentle swiveling action of the wrist" [74, p. 119] to gather the algae scum onto the tool. A similar technique has since been reported at Bakoun, also in Guinea, about 500 km north of Bossou [75]. Like pestle-pounding, to date it has been observed only in these Western populations, whereas Humle et al. [74, p. 117] remark that "the species of *Spyrogyra* sp. occurs elsewhere. For example, *Spyrogyra* sp. occurs at Mahale, Tanzania (Nishida, personal communication) and a young adult female migrant into the Mahale M group was observed feeding on algae by hand without the use of a tool (Sakamati 1998 [76])".

Boesch et al. [75, p. 4] describe the most challenging forms of algae gathering at Bakoun. Unlike at Bossou where it is fished from the water surface, the algae grows up from the river sediment into the water: "the chimpanzees were observed to fish for algae at sites where the algae occurred in large accumulations at the bottom of the river bed". Tools were sometimes extremely long, up to nearly 2 m for tools with small hooks remaining on them, and up to over 4 m for straight tools (Fig. 3a). This task entailed considerable manipulative skill, else the slippery algae would slide off the tool.

Bandini and Tennie [69] conducted an experiment that they asserted "directly tested the ZLS hypothesis on algae scooping, a wild chimpanzee tool-use behaviour", by providing chimpanzees in a UK zoo with "ecologically relevant materials of the wild behaviour" (p. 1). In practice, this was a bowl of water directly on the other side of the cage mesh, on the surface of which curved crusts of bread were floated. The chimpanzees were provided with short sticks

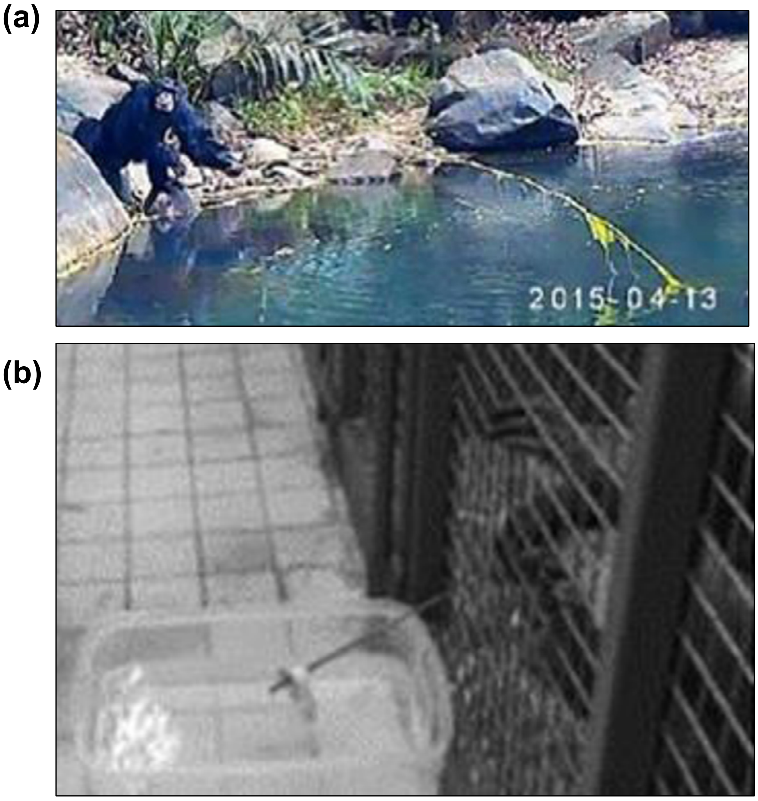

Fig. 3. (a) Algae scooping with a long bamboo wand in Guinea [75]. Scooping bread from a bowl of water by a captive chimpanzee [69]. See text for full descriptions.

and within the first 10 minutes two chimpanzees in separate groups used the sticks to gather crusts from the bowl of water.

The authors concluded that “Our results demonstrate that the wild form of scooping behaviour re-appeared independently in two naïve chimpanzees” (p. 13). Elsewhere they talk of “slight differences in the overall physical setup between our experiment and the wild” (p. 11). The contrasts highlighted in Fig. 3 surely question this. What the chimpanzees did in the experiment will likely surprise nobody who knows the species at all well. The question of whether wild chimpanzees rely on cultural transmission to acquire the behaviour, and copy what others do, or whether each chimpanzee invents the skill as the authors suggest, remains open given the substantial differences between the two contexts. Maybe the authors are correct in their interpretation,[5] but the contextual contrasts are so gross that their results and conclusion remain uncompelling.

3.5.3. Termite fishing at termite mounds

Teleki [77] provided a particularly helpful analysis of wild chimpanzees’ techniques for fishing termites from their mounds, because he attempted the component skills himself to help gauge their difficulty. He noted the narrow, winding termite tunnels, just a few milllimetres in diameter, are sealed at the mound’s surface by a soil plug, so a chimpanzee first has to find and remove this to reveal a tunnel. Having fashioned a suitable probe, this must then be carefully inserted and manipulated using a precision grip so it will wind down the irregularly shaped tunnel. Hunt [78, p. 409] reports such tools up to 2 m long. The fishing tool must then be carefully withdrawn to avoid detaching the termites biting on to it. As the tool is withdrawn the termites are removed directly by the lips, or using the fingers of the other hand to slide them to the mouth.

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[5] Note that in any case, Whiten et al. [12,13] did not include algae scooping in their list of putative cultural variants of chimpanzees, because its distribution was inferred to be likely shaped by local ecological opportunities.

Attempting to first locate a tunnel, Teleki [77] reports (p. 586) that he “applied several experimental procedures: examining in minute detail all crack patterns, protuberances, depressions and other topographic features in the clay”. But “after weeks of searching for the essential clue, I had to resort to scraping mound surfaces with a jackknife until a tunnel was inadvertently exposed. My inability to find any physical features which could serve as visual cues eventually led me to realize that chimpanzees may possess knowledge far beyond my expectations”. This was despite Teleki having a brain three times larger, plus more dextrous hands, and benefitting from having seen his subjects’ termite fishing, unlike any chimpanzee who had to discover all this by itself. He noted that “chimpanzees require a prolonged learning period (i.e. 4-5 years) to gain proficiency in this technique (van Lawick-Goodall, 1970 [79]).”

Concerning selection of appropriate tools, he concluded that “the specifications are in fact surprisingly stringent: if the vine or grass selected is too pliant, it will buckle and collapse .... if on the other hand, the object is too stiff or brittle, it will catch on the tunnel walls and either break or resist entry to the necessary depth. An intermediate range of qualities must therefore be selected” (p. 586).

Next attempting fishing itself, Teleki reported, echoing his experience of locating tunnels, that “only after weeks of nearly total failure ... did I finally begin to grasp the problems involved ... a newly opened tunnel requires subtle techniques ... the probing object must first be carefully and dextrously inserted to a depth of about 8-16 cm, with appropriate turns of the wrist so that the object navigates the twisting channel. The probe must then be gently vibrated with the fingers during the prescribed pause, for without this movement the termites may not be stimulated into biting firmly onto the probe” (p. 588). Teleki devoted several further sentences to the nuances of successful fishing.[6]

Hopper et al. [80] reported on chimpanzees’ first responses to an artificial termite mound provided in a zoo. The mound echoed the shape of mounds in the wild, usefully allowing the public to watch chimpanzees using probes to feed from it, illustrating a version of their behaviour in the wild. However, in respect of relevance to the ZLS hypothesis, the set-up departed significantly from termite fishing in the wild, as described by Teleki and others. In particular, (i) the tunnels were already open, whereas in the wild they are plugged and, as Teleki discovered, barely visible; (ii) the tunnels were 4.5 cm wide rather than the approximate 0.5 cm in the wild, so chimpanzees were able to poke large stiff sticks directly down the open tunnels; (iii) the tunnels were also straight, so jamming in a stiff tool using a power grip would suffice, unlike the delicate technique that Teleki found so challenging; and (iv) the rewards were fluids like ketchup, that merely required dipping the end of a stick in, unlike the nuances of getting termites to bite and avoiding losing them on tool withdrawal.

Hopper et al. did not claim that their experiment offered a true analogue of all this, but rather that it confirmed more broadly that chimpanzees could create and modify sticks for the purpose of extracting food from tunnels in a mound. However in their discussion the authors nevertheless then related their results to the ZLS concept, saying “If probe tool manufacture and modification is within chimpanzees’ ‘Zone of Latent Solutions’ [sensu Tennie et al., 2009 [50]]...” and Motes-Rodrigo and Tennie [81, p. 1445] asserted that “Several studies have now shown that wild ape behaviours spontaneously reappear in culturally unconnected populations that have never observed a model demonstrate the behavioural form in question”, citing Hopper [80] in support. I suggest the latter study did not, and should not, be seen as demonstrating naïve chimpanzees’ capacity to individually acquire the particularities of termite-fishing in the wild. A later study with the artificial mound [82] was framed by analogy to another form of termite fishing in the wild, discussed next.

3.5.4. Termite fishing from subterranean nests

Sanz and colleagues [83,84] reported results based on use of camera traps to record termite fishing of chimpanzees at six sites in the Congo Basin, describing two different techniques and associated tools to deal with different structures. For above-ground mounds, chimpanzees often used a twig to open a tunnel entrance, removing about 1 cm of

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[6] Teleki’s [77] full description of termite fishing continued: “if the vibration is performed too lengthily or roughly, there is an excellent chance that the probe will be cut through by the mandibles while still in the tunnel. When these preliminary actions have been correctly performed, the probe, presumably with dozen of termites now attached, must be extracted from the tunnel. Once again there are nuances to be observed. If the object is too rapidly or clumsily pulled out, the insects are likely to be scraped off along the sides of the tunnel, which then yields nothing but a shredded probe. The hand motions must be reasonably but not overly swift and, once started, uniformly fluid and graceful. If the tunnel is particularly tortuous (a feature that can be determined during insertion of the probe), the success of the catch can be assured by a slow twisting of the wrist while the probe is pulled out.” (p. 588).

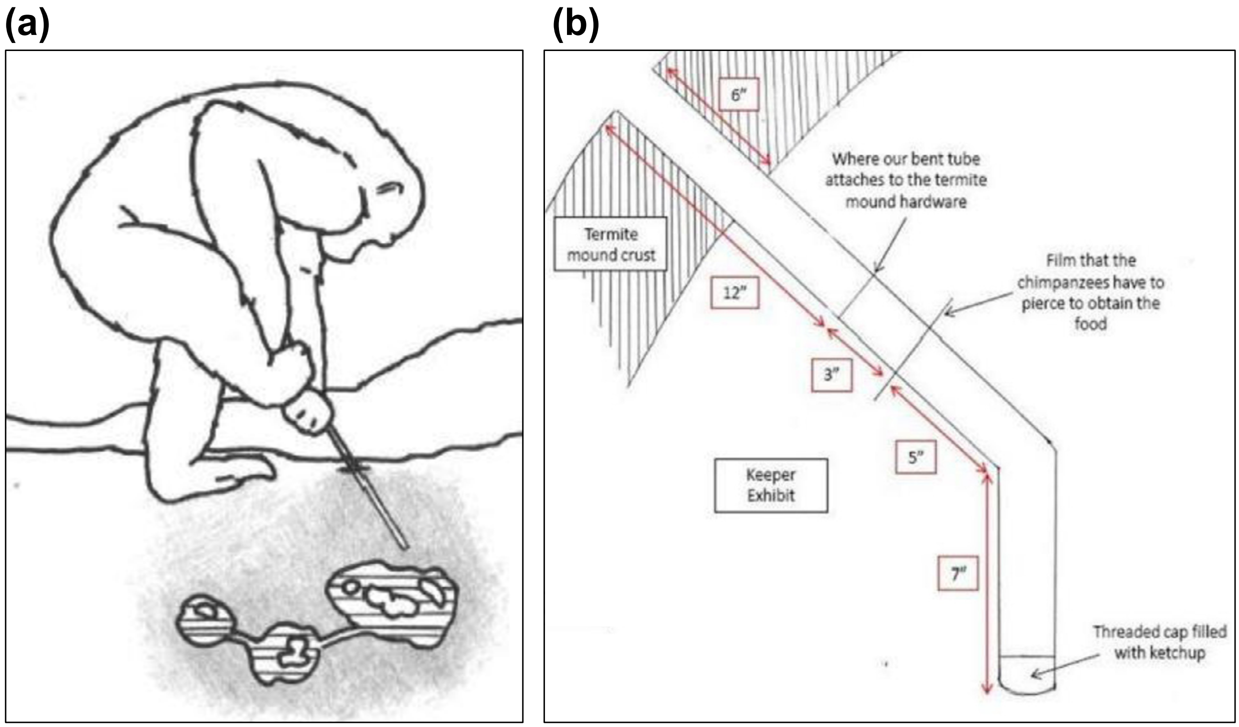

Fig. 4. (a) Wild chimpanzee making a tunnel through the earth to a subterranean termite nest, preparatory to passing a second tool down the tunnel to fish termites out [83] (drawing by D. Morgan, with permission). (b) Diagram of modified termite mound to test for tool-set use in captive chimpanzees [82].

clay in this way. They fashioned a fishing stem by removing leaves and stripping the stem through partially closed teeth several times, creating a brush tip. This feature is particularly effective, when inserted into tunnels, to harvest the soldier termites that attack the inserted probe. The other technique is for below-ground nests connected by series of tunnels. At these, the chimpanzee uses a previously discarded stout stick, or one brought to the site, to pierce downwards into the underground structures (Fig. 4a). This appears hard work, as both hands and one foot may be applied to force the stick down through the compacted earth, reminiscent of digging with a spade. A brush-tip stem is then carefully passed down the tunnel to harvest the soldier termites responding to the intrusion. Puncturing sticks were about 1 cm thick and averaged 41 cm long, with a maximum at one of the six sites surveyed of 52 cm. Fishing tools averaged 43 cm [83].

Noting the existence of this form of tool set in particular, Bernstein Kurtycz et al. [82] modified the zoo mound used earlier [80] by adding a 45-degree bend to each tunnel, plus a cellophane barrier across the tunnel at a depth of about 35 cm (Fig. 4b). This sought to embody aspects of both subterranean puncturing, and fishing in tunnels that are not straight. It required two tools to be used sequentially: one strong and rigid enough to puncture the cellophane, and another flexible enough to pass round the bend and dip into the ketchup. Appropriate tools were provided in the form of rigid PVC rods and strips of cardboard.

Successful harvesting of ketchup was first achieved by the necessary sequence of insertion of rigid and then flexible tools in the third of ten half-hour experimental sessions. Estimating from the authors' Fig. 2, chimpanzees dipped one or other kind of tool into tunnels about 50 times on average, indicating much trial and error before the first success. Chimpanzees had to be tested in groups, so that after the first success it was not possible to discriminate the extent of social versus individual learning involved in later successes. The authors noted that starting with a rigid tool decreased across sessions, indicating that within the total five hours of the study, the participants "could not see the causal purpose for the rigid tool. Taken together, findings suggest that, while at least one chimpanzee did innovate the tool-set form, the behavior did not stabilize." (p. 303).

The authors conclude that "the chimpanzees we tested did use the tools to extract rewards, and did use the tools in the required order, showing that the form of this tool set (its correct sequence) falls generally within the ZLS of chimpanzees" (p. 306). Thus they did not claim specifically that this was a representative analog of subterranean termite fishing in the wild. However in the introduction presenting the rationale for their study, they first describe the findings in [80], then say that "In order to test for tool set re-innovation, we extracted the relevant components of the behavioral and artifact forms from wild tool-set behavior" and "From the start, we attempted to create conditions as similar to the wild as possible" (p. 291). Thus the reader is left with the impression that a reasonable analogue has been tested.

As in [80], in [82] the chimpanzees were presented with a mound with large open holes that invited tool insertion. This contrasts particularly markedly with subterranean puncturing in the wild, where to be consistent with the ZLS hypothesis we would have to imagine a chimpanzee pushing a stout stick down, over 30 cm through the earth, starting from an unmarked soil surface. The causal opacity of doing so in this context is striking and one reason to suspect this is the result of cumulative culture. In addition, the chimpanzees in the experiment had already learned to probe for rewards in the mound. Ironically, it thus cannot be excluded that what [82] documented was a modest case of cumulative culture, with participants building on their earlier knowledge of probing to add the puncturing element. Whether they would have invented use of the tool set if a barrier had been included at the outset and required penetration of 30 cm of earth rather than a sheet of cellophane, with tunnels not open but covered by earth, we cannot tell.

3.5.5. Nutcracking

The nutcracking of chimpanzees of West Africa mentioned in section 3.5.2 involves placing a nut that is too hard to crack orally on a stone anvil or tree root and bringing a stone or wooden hammer down on the nut with a skilled force that cracks the shell but does not pulverize the desired kernel inside. Three quite different studies tested the likelihood that naïve chimpanzees would crack nuts when faced with the raw materials.

First, chimpanzees aged two to six years old in a Ugandan island sanctuary were presented with suitable stones and oil palm nuts for cracking in two 30-60 minute baseline trials, in the second of which an already-cracked nut was included to mimic such learning opportunities in the wild [85]. One five-year-old, Mawa, immediately cracked nuts, consistent with acquisition whilst earlier kept as a pet, as nut-cracking by Ugandans is common. No others showed any indication of cracking behaviour. Eight were then assigned to an experimental group that witnessed Mawa and a familiar human crack nuts, and six to a parallel control group merely exposed to the materials for the same amount of time. Four of the five experimental subjects aged over three years acquired nut-cracking after watching the models whereas no control subjects did. When all were exposed to the model, all nine more than three years old acquired nut-cracking. Four other studies have investigated social learning of nutcracking in chimpanzees, without including any asocial control conditions [86, for a review].

Neadle et al. [87] offered 13 adult chimpanzees in a zoo macademia nuts, a wooden anvil and a large, tethered, log hammer in "extended" baseline periods of unspecified length, first with whole nuts and later with several cracked nuts. No chimpanzee cracked nuts, but unlike the Uganda study above, no nutcracking occurred after human demonstrations either. The authors suggest that one explanation for the difference is evidence from the wild that if nutcracking is not learned within a sensitive period lasting around five years, it is not acquired later [88]. Another possibility is that the model was a human, unlike Mawa in [85].

The third study was conducted in the wild, so arguably the most ecologically valid of these tests. Koops et al. [89] tested a population of wild Western chimpanzees known not to nutcrack, unlike other nearby communities in the region. The same raw materials exploited by the latter, including both oil palm and coula nuts, were presented to the naïve community for over 700 days at two locations where they would encounter them, and already-cracked nuts were also provided. Responses were monitored via camera traps. Chimpanzees explored the objects through close observation, sniffing and touching, but did not eat or crack any nuts. The concern that longer exposure might have generated different results was addressed by the finding that exploratory interest did not increase, instead waning over time.

All three of these quite different experiments converge on the conclusion that individual discovery of nutcracking does not readily occur in chimpanzees – a finding consistent with its absence across most of chimpanzees' range in Africa despite the availability of suitable raw materials.

By contrast, Bandini et al. [90] reported that at least four orangutans in two captive populations spontaneously used logs to crack open macadamia and coula nuts provided on the hard floor. This seems a striking finding insofar as we are faced with the curious contrast of no spontaneous nutcracking in diverse kinds of experiments with chimpanzees, a species that cracks nuts in the wild, versus spontaneous nutcracking by some orangutans, a species that does not crack nuts in the wild. But of course there is always a first time: once, a wild chimpanzee cracked the species' first nut. However, the ecological validity of the orangutan behaviour is restricted insofar as the materials were provided directly to the participants, with little else for them to do but attempt to extract edible fractions.

3.5.6. A way forward?

It seems clear that at present there is a wide gulf between most of the studies and conclusions derived from captive populations reviewed above, and field studies. Field researchers are dismissive of or simply ignore interpretations from these efforts with captive chimpanzees on grounds of inadequate ecological validity, often interpreting their own findings in the wild as evidence instead of limited cumulative culture [46,84,91]. I propose that in addition to any further, ecologically realistic tests in the wild, a potential resolution of this scientific impasse should be that results from experimental tests of invention, whether with captive or wild participants, be regarded as valid, compelling and publishable only so long as fieldworkers who know the behaviour in the wild are prepared to collaborate and put their name to co-authoring the work. This remains too rare [80].

4. Is imitative copying unique to humans and is it the key to cumulative culture?

At a broader level than the recent focus on a hypothesized ZLS, the 'ratcheting' hypothesis put forward three decades ago [3], and popular since, suggested it is high fidelity imitative copying that maintains cultural traits in place between the innovative events that ratchet up human cumulative culture, whereas a lack of this imitative capacity denies cumulative culture to non-human animals. For economy I dub this the imitative copying hypothesis (ICH) of CCE. Early experimental findings with captive chimpanzees were interpreted as evidence for only a more limited form of social learning called emulation [14,92], which in broad terms involves recreating desirable *results* of others' actions, rather than replicating the *forms of the actions* themselves. This perspective now also merits a critical appraisal.

4.1. Imitation and emulation: comparing like with like

Over the three decades since ratcheting and the ICH were formulated, both imitation and emulation have been conceptualised and defined in some very different ways [61]: so much so, that disagreements over what is and is not distinctively human have arguably been shaped as much by these alternative conceptions and semantics as by key empirical findings themselves. Perhaps most significantly, many who conclude that chimpanzees and other species do not and cannot imitate restrict the concept to bodily or "motor" imitation [14,50,93–95]. This contrasts both with common everyday usage, and the concept of imitation as typically applied in child research, where most studies of human imitation occur. This is well illustrated in the phenomenon called 'over-imitation', in which children copy even actions that can be seen to be causally ineffective in the contexts involved. In virtually all the 50 studies reported since this phenomenon was discovered [96], imitation is not identified by bodily matches to what the child witnessed, but by matches to what is done with tools or other objects affected [97]. For example in the study that first labelled 'overimitation' [98], imitation was identified when children copied actions on puzzle boxes, described in phrases such as "rotate metal basket 180° using its side handle" and "pull bolt from base of plastic box by using wooden handle". Such descriptions ignore what bodily motions created the forms of these actions.

If equivalent criteria are applied to chimpanzees, then controlled experimental evidence shows not only that such imitative results occur, but they can drive cultural diffusion across, and even between, groups. This evidence utilizes the powerful 'two action-method' in which each of two alternative action sequences, differing in form, can achieve the same rewarding outcome. The alternatives are initially 'seeded' by training a single model in each of two or more groups, then tracking whether the alternatives spread differentially in the groups in which they were seeded via this model.

Fig. 5 illustrates this approach in three different experiments with Yerkes chimpanzees [99–101] and for two with Bastrop chimpanzees, where in each case the two different techniques spread across a first group and then to a second

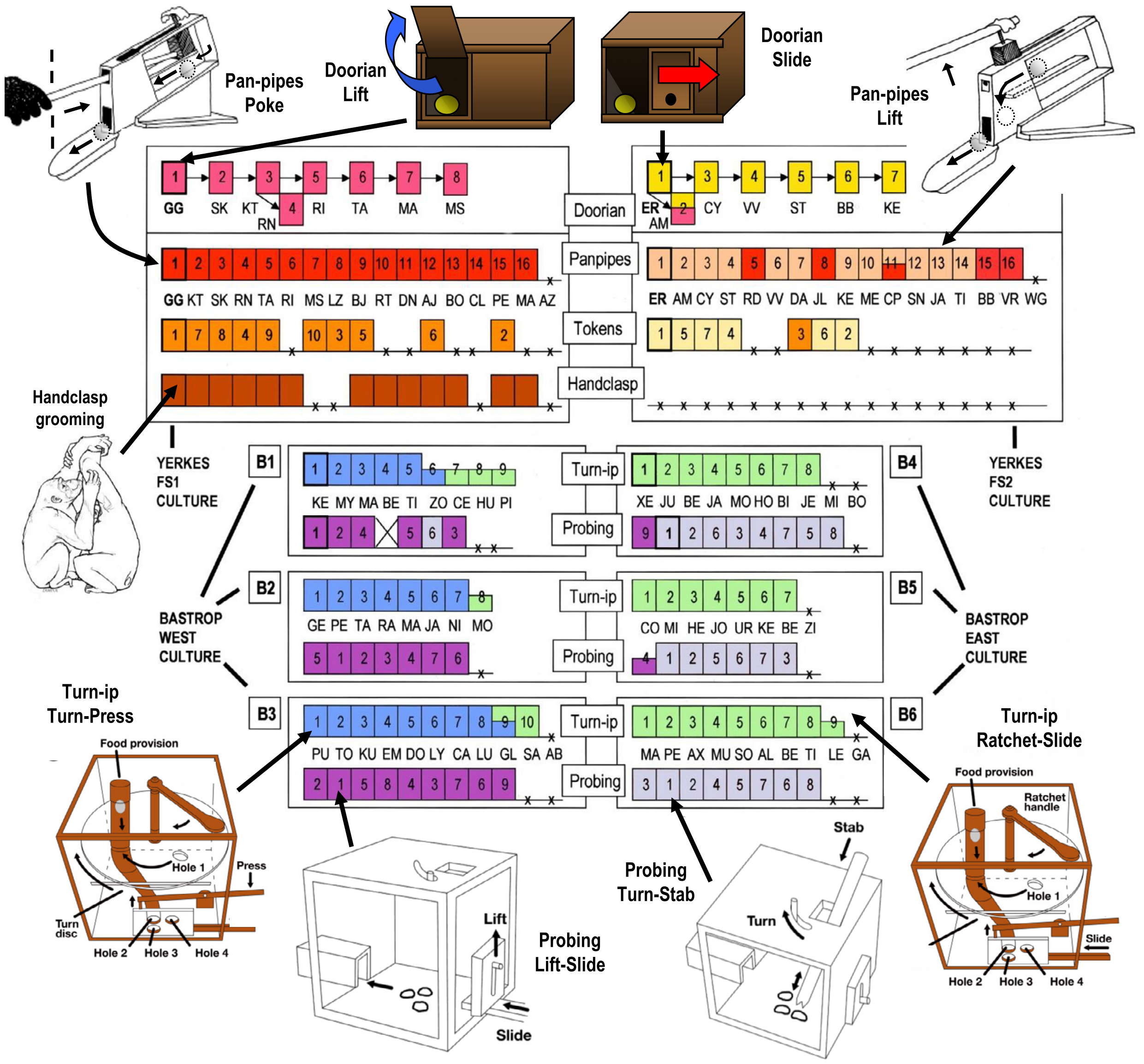

Fig. 5. Results of two-action cultural transmission experiments with chimpanzees. Spread of experimentally seeded alternative forms of tool use and other foraging techniques, generating four chimpanzee ‘cultures’, each constituted of two or more such variants. At each pair of locations, alternative techniques were experimentally seeded in a single individual, after which they spread to be the common technique in that group. Each block with a letter code represents a single chimpanzee, with colour coding corresponding to the alternative techniques seeded in the first individual in each case. At Yerkes, Row 1 = *lift* versus *slide* methods to open door in ‘doorian fruit’, run as a diffusion chain [100]; Row 2 = *poke* versus *lift* ‘panpipes’ techniques spread in an open (unconstrained) diffusion [99]; Row 3 = *bucket* versus *pipe* posting option for tokens in an open diffusion [101]; Row 4 = hand-clasp grooming, which arose and spread spontaneously in only Yerkes FS1 community. At Bastrop, Row 1 = *turnip-slide* versus *turnip-ratchet* techniques, Row 2 = *fish-probe* versus *fish-slide* techniques, used to extract food from two different devices; each technique spread to a second group (middle, groups B2, B5) and then a third (bottom, B3, B6) [53]. Numbers indicate order of acquisition. Redrawn from data in [53].

and third, with high fidelity [53]. Fidelity was not perfect but *more than sufficient* to sustain the differences between alternative cultural variants – which is what the ratcheting hypothesis argues is missing in non-human species. Following the conceptualisation in child imitation studies noted above, the matching to the original, seeded model would be described as “imitation”. This is consistent with the conception in [102], reporting imitation in chimpanzees described as ‘enculturated’ (human reared[7]), of actions described in a similar way, such as “use stick to drum on can and open it” and “spin roller, use roller to flatten play-doh” (p. 1704).

Authors arguing that chimpanzees do not imitate have suggested that results like those illustrated in Fig. 5 may instead reflect emulation, if the participants are learning only about the particular ways in which the tools and other objects move [50]. An alternative conception (as in everyday speech and child research) is that how agents move tools and how these move further objects be regarded as part of the form of each particular action, considered in the round. In the pan-pipes experiment (Fig. 5), raising the stick tool, making it lift a blockage up to release the reward, versus poking the tool forward to drive the blockage so it knocks the reward down, are two different forms of action that an observer of them may replicate, with repeated replication generating alternative traditions. Whatever the precise details of the learning process, the form of each alternative action is replicated as it is culturally transmitted across a population.

Accordingly, Whiten et al. [61,103] suggested that a superordinate category of ‘copying’ should be helpful in reporting the cultural transmission of such variant techniques (Fig. 6), leaving open for further research just what is replicated by ‘copying’ in the course of cultural diffusion. Copying may be of various components of bodily actions, tool movements and/or resultant changes in objects or other parts of the environment. A core interest in cultural transmission studies is the perseverance of such copies, whatever the finer distinctions in how the learning is taking place.

4.2. ‘Ghost’ experiments

Differentiating among the alternatives nested within “copying” in Fig. 6 is challenging. It has been pursued through ‘ghost experiments’ in which only the object movements concerned are witnessed. Tomasello [92] suggested that when a young primate watched its mother roll over a log to reveal insects beneath, the youngster might learn just as well if a wind rolled the log. Hopper et al. [104] accordingly engineered a display in which the blockage in the panpipes rose up as if lifted, and even a display in which the stick tool made this happen, but in neither case was a chimpanzee responsible. No chimpanzee learned from this, contrasting markedly with the results of the cultural transmission experiment in which they could learn from the actions of a conspecific (Fig. 5). This leads to the conclusion that for

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[7] According to Wikipedia, *enculturation* “describes the process of learning one’s own culture, acculturation denotes learning a different culture, for example, that of a host”. The term “enculturation” was perhaps first used in this sense in the context of animal culture by Imanishi [189], in interpreting the early evidence for the spread of foraging innovations via social learning in Japanese monkeys. Finding that chimpanzees raised in intimate relationships with humans were more likely to imitate humans than those mother-reared, Tomasello et al. [102] gave the term a more elaborate twist, perhaps more akin to acculturation, but suggesting further that such cross fostering changed fundamental aspects of social cognition, such that these apes would show imitation, whereas those reared by their mothers in captivity or in the wild would not. Call and Tomasello [190] later developed this idea more fully. However in commentaries on Tomasello et al. [3], Boesch [191] and Whiten [192] independently offered very similar alternative interpretations of the findings. Essentially these were that rather than “enculturated” chimpanzees being the odd ones out in the trio with captive, and wild, mother-reared individuals, the captive chimpanzees might be the odd ones out. These commentaries argued that being reared in a rich human environment simulates experiences in the wild where youngsters find extensive social learning of great utility. By contrast, captive apes living in relatively barren environments have few opportunities of these kinds and their social learning potentials may thence atrophy. Bering [193] offered a deeper and more thorough critique of the “enculturation hypothesis”, concluding that “it is premature to state that human-raised great apes have undergone any meaningful alteration of their species-typical cognition. Many scholars, however, continue to promote the hypothesis, and to view the single experimental study on which it was founded, as prima facie evidence of its validity. In addition, those researchers advocating the enculturation hypothesis have not explored the theoretical biology deeply enough. Advocates must explain more clearly how it is that the cognitive and psychological adaptations of humans, a derived species, can come to appear in the cognitive phenotype of a conservative species in response to the latter being exposed to social behaviors that were probably absent in the common ancestor” (p. 210). Bering suggested an alternative “apprenticeship” hypothesis, in which chimpanzees reared in intimate relationship with humans simply learn that it is profitable to attend closely to human actions and learn from them. I find Bering’s analysis the more compelling. Nevertheless, the often-impressive imitative copying of human-reared chimpanzees continue to be dismissed as irrelevant to what “real chimpanzees” are capable of [e.g. [51,52]]. I suggest instead, that (i) in line with Bering’s analysis, such experiences are inherently unlikely to magic a capacity for imitation out of a brain that lacks some innate foundation for this; (ii) the explanation for the so called enculturation effect may be as Bering proposes, and sometimes even simpler – that these chimpanzees are simply more familiar with humans and treat them more like conspecifics; and (iii) because the actions copied are often so clearly novel for chimpanzees (such as looking in a mirror and applying lipstick to one’s lips: Hayes and Hayes [123]), the rich literature on such effects is in fact telling about such capacities in apes. The other side of this coin is that tests of imitation in “non-enculturated” apes that report little copying of unfamiliar humans in contexts quite unlike those claimed to represent equivalence in child testing (e.g. [194]) can be highly misleading [195]. Tests involving copying conspecifics may tell a very different story (Fig. 5).

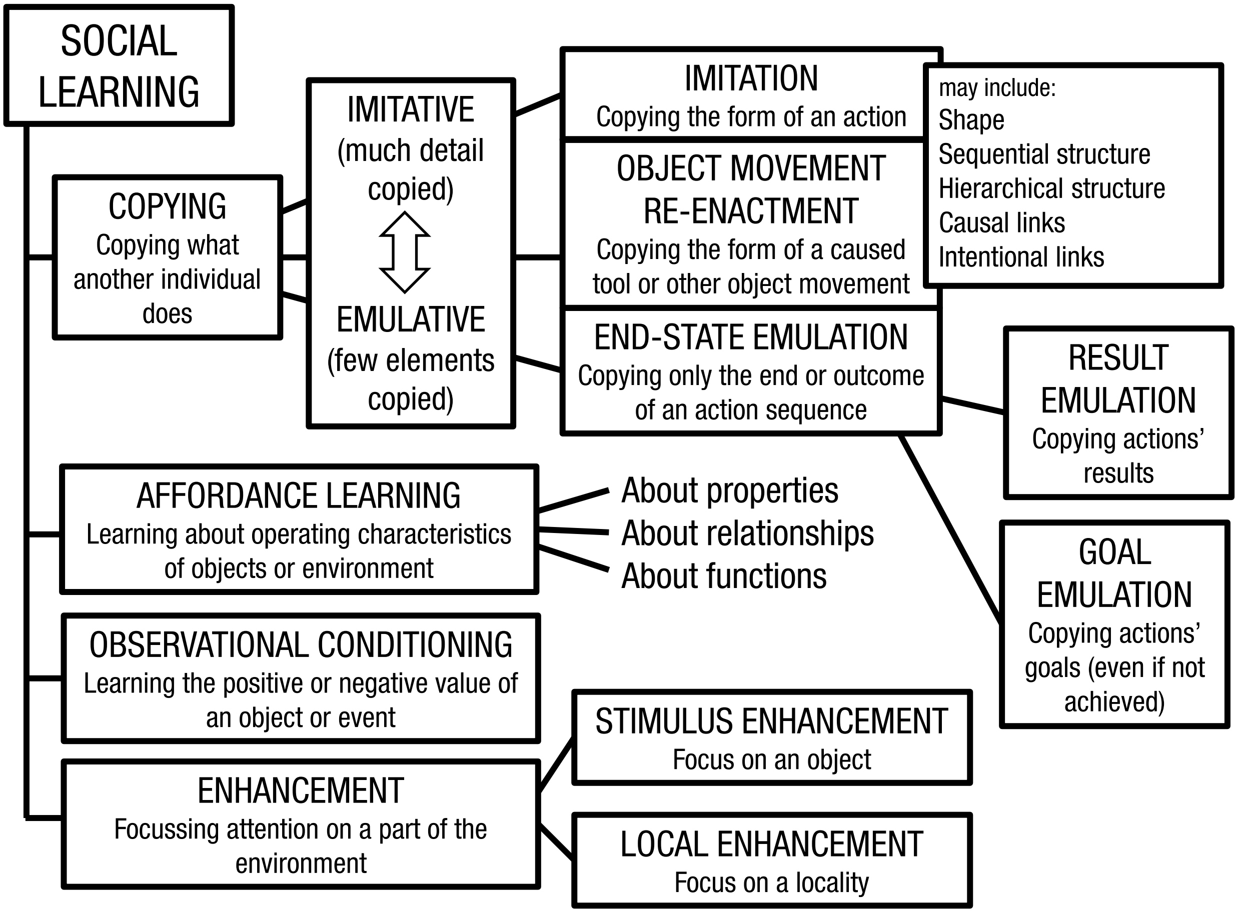

Fig. 6. A taxonomy of forms of social learning, distinguished by what the learner learns (after [61,103]). Each is here briefly defined. Copying of what another individual does may involve imitation of the form of actions, or re-enacting the form of resultant tool or other object movements, or some combination of these. Matching between model and learner in these respects may include the form of an action's shape in space and time (e.g. the way a hammer is wielded), its results (an object is smashed, or two objects nailed together) its sequential or hierarchical structure (e.g. a particular pattern of hammering nails into a substrate), and inferred causal (hammering force drives nails in) or intentional links (intent was to hammer nails to create a certain effect) between components, or some combination of these. Emulation may involve copying only the observed result of another's actions, (two objects got nailed together) or copying their assumed goal, in cases where they are perceived to pursue such a goal yet not achieve it. The distinctions in this diagram were hatched through debates in comparative cultural cognition. In developmental psychology, 'imitation' is largely equated with 'copying' in this diagram, and splits within this category appear to be of less interest and debate.

an action as complex as this, it is important for chimpanzees to observe a *model acting* to create a desirable effect, and thence acquire the technique witnessed.

4.3. 'Copying' and 'culture-dependent traits'

Tennie et al. [51,52] have more recently shifted their claims of human uniqueness in social learning from "imitation" to a broader concept of "copying observational learning" (also called "form-copying social learning") a terminology thus seemingly consistent with the conception of copying introduced earlier, in [103] (Fig. 6). But the authors' argument that apes and other animals do not learn in this way seems no less puzzling than the more restricted hypothesis focused on imitation, because the central rationale of two-action experiments, like the five illustrated in Fig. 5, is that they seed different groups with models displaying actions differing in form, and test whether these spread to become incipient traditions or cultures replicating these different forms. Such outcomes have been identified in diffusion experiments ranging from those recently documenting faithful cultural diffusion of alternative foraging techniques across populations of hundreds of great tits in the wild [24,105,106] to earlier experiments spanning a diversity of avian and mammalian species reviewed in [27] with further additions in [9], including some on wild primates [107].

Further claims that "culturally dependent traits", defined by "the presence and observation of the form of at least one trait at time t is required for the presence of the same form of at least one trait at time t + 1" are also unique to human culture [51, p. 429], add confusion. The alternative traditions illustrated in Fig. 5, and in other two-action cultural diffusion experiments in the two reviews cited above, are caused by (so causally dependent on) whichever of the two experimentally seeded alternative action forms that individuals tend to witness and subsequently adopt. In this sense they are thus 'culturally dependent'.

It emerges that what these authors mean by a 'culturally dependent trait' is not one that is simply 'dependent on culture' in the sense above, but one that is beyond a species' ZLS as conceived by the authors. However this simply brings us back to the multiple problems in the coherence of this concept and its testability outlined above in sections 3.1–3.5. One article by Motes-Rodrigo and Tennie [81, p. 1445] refers to "the products of copying social learning, namely culture-dependent forms" and elsewhere "culture dependency (and consequently copying)". Confusingly, the first of these is asserting that copying necessarily leads to or entails culture dependency in the narrow "outside a species' ZLS" conception of the authors, whereas the second assertion *reverses* the direction of the supposed causal arrow, stating that culture dependency necessarily implies copying. In addition to this confusing argumentation, neither implication follows. Concerning the first, copying may simply sustain long term traditions without necessarily generating CCE, and indeed this may characterize many of the traditions of chimpanzees and other animals. Concerning the second, there has been no supposition across the literature on cumulative culture in animals such as in pigeon homing [41] and seasonal migration [42], described more below, that they necessarily rely on copying the actions of others: simpler forms of social learning such as local enhancement may sometimes suffice.

4.4. How significant are bodily imitation and copying in cultural transmission and cumulative culture, whether in humans or other species?

As reviewed above, a capacity for imitation is commonly argued to be the unique human factor maintaining traditions with high fidelity over generations [e.g. [3,93]], so permitting repeated innovative improvements to be incorporated into cumulative cultures. But how much of human cultural transmission actually involves or requires *bodily* imitation? To my knowledge nobody has attempted to provide an empirical answer to this crucial question and the assumptions it addresses. None of the 49 cases of diffusion of innovations in human culture in Rogers' [108] influential analysis, nor the many in Basalla [109], appear to rely on bodily imitation. Of course bodily imitation is inherently required for copying pure body movements such as gestures and dance moves. But in acquiring much of our 'cultural know-how', such as widespread technologies like cooking, weaving, basket-making, pottery and weapon-making, any bodily imitative element is typically intimately meshed with copying resulting movements of objects, including the actions of tools on other objects. The spatio-temporal forms of tool actions can be copied just as can the forms of bodily actions and they often form a complex whole. Thus the broad conception of "copying" (Fig. 6) may represent common transmission processes better than does "imitation", especially in the narrow bodily sense, in much of material culture. And as described above, copying can show sufficient transmission fidelity for alternative forms of action to diffuse both across and between groups of chimpanzees (Fig. 5). Modelling of cultural transmission processes led to the conclusion that in any case "exact copying is fragile in an (even slightly) noisy world" [110, p. 20170050].

These considerations have much in common with Byrne and Russon's [111] concept of 'program level imitation', defined by copying taking place at the level of an overall, hierarchically-organised program of action (including actions applying tools or achieving particular environmental results), irrespective of any details of bodily imitation. Although these authors applied the concept particularly to observations of great ape behaviour such as rehabilitant orangutans' copying of peoples' application of kerosene to rekindle fire embers, followed by fanning with a pan lid, they added that "We believe that program level imitation is the major contributor to the acquisition of skilled instrumental behaviour even in humans, and that action level [bodily] imitation plays a minor role" (p. 682). Little explicit experimental testing for PLI has been conducted in apes or other animals, although copying of alternative sequences of actions to disable protections on an 'artificial fruit' was demonstrated in chimpanzees [112]. Copying of alternative hierarchical organizations of the same set of tool-based action elements to extract a reward from a complex puzzle box has been shown for human children [113] and in relation to the present discussion a version which dissected the most important parts of what could be witnessed is telling [114]. In this study, children watched different video clips of either of two hierarchically-organised ways of using tools to open the box. Video clips that showed only the tool's action on the box were much more effective in eliciting both copying of the alternative witnessed and applying it successfully than a view of the hand-plus-tool actions alone. Viewing the whole complex of hand, tool and object movements created the highest fidelity copies.

4.5. Is bodily imitation absent in non-human animals?

The assertion that bodily imitation *per se* is not within the capacity of non-human animals [e.g. [93]] merits challenge in its own right. Experiments with pigeons and quail long ago demonstrated that birds who witnessed conspecifics using either beak or foot to press a treadle to obtain a food reward, tended to use the same bodily technique [115,116] (see [117] for a review of these and numerous other related avian experiments, some by Heyes and colleagues). Similar results were reported for marmosets [118] and vervet monkeys [119] copying either the oral or manual means of opening an artificial fruit they witnessed a conspecific model use. Likewise, chimpanzees that copied bizarre, novel means of creating results such as a light switching on used the same bodily actions as the human model (touching with the head, or foot, or bottom) [120][7]. They tended to do this only so long as the model had his hands free, and so could more naturally have used manual actions, yet chose the bizarre alternative witnessed – so called 'rational imitation' [121]. A version for dogs showed copying of the uncommon canine use of a paw (rather than mouth) to operate a lever to release a food reward, but only so long as the model did not have the more natural oral approach blocked by holding a ball in its mouth [122].

A greater range of bodily action matching was revealed through training a chimpanzee to match a variety of human actions on command and then testing for imitative copying using an array of novel, untrained actions such as clapping the back of the head [123]. Experimental procedures in this early work were ill-specified, but later, rigorous replication showed that coders blind to which of a battery of 48 actions was shown by a human could identify a significant number matched by two chimpanzees [124][7]. A different coding method, but the same battery of actions, showed that an orangutan was judged to produce 58% full imitations and 32% partial imitations of the battery [125][5]. Hayes and Hayes [123] also described a range of imitations of human actions by this chimpanzee in their home, such as looking in the mirror and applying lipstick to her lips, as Cathy Hayes had done.

Consistent with these findings, a recent study of wild chimpanzees [126] revealed differences in the action patterns applied to both above-ground and below-ground termite fishing across multiple central African research sites. These experienced fieldworkers judged that the differences could not be explained by ecological factors. Since the variation included different bodily postures and actions adopted in fishing, it was concluded that "given the community specificity of the combinations of elements ... our results are best explained by a high-fidelity social learning mechanism" (p. 5).

Gestures, whether arbitrary and/or meaningful, may constitute a particular and significant category of actions not so spontaneously imitated by chimpanzees. Chimpanzees failed to copy a conspecific trained to perform a bizarre 'praying' posture to be given a reward [127] and bonobos did not copy a human's handwaving gesture displayed before opening a puzzle item, whereas young children did [128]. One interpretation is that chimpanzees are not disposed to copy such gestures *per se*, particularly where they appear physically, causally unconnected to rewarding outcomes in the world. Heyes [94.95] has made allied suggestions, a speculation consistent with the fact that although ape gestural repertoires are extensive, the evidence to date suggests they may be largely innately shaped, many of them even shared across all the great ape genera [129]. Chimpanzee imitation might be aptly characterised as more pragmatic than humans', focused on actions that can be seen to physically cause desirable payoffs. Findings that chimpanzees are most imitative in contexts where one object is made to act on another (as in tool use) are consistent with this [130]. Such apparent contrasts merit further focused experimental testing.

5. Fidelity of social transmission and its varied manifestations

The hypothesis that low fidelity transmission is the block to cumulative culture in animals is typically framed in terms of a deficit in short-term processes of social learning, particularly a lack of imitation or 'form copying' [50–52,87,90,131,132]. I suggest that the concept of transmission fidelity begs more conceptual analysis and dissection in the context of long-term cultural stability and change.

5.1. Dissecting and evaluating transmission fidelity

Charbonneau and colleagues [133,134] unpick three different senses of ‘transmission fidelity’ that need to be clearer in such hypotheses: episodic fidelity, referring to a particular episode of transmission; mechanistic, referring to the mode of transmission, such as imitation or emulation; and generalized, referring to the capacity of some species or ensembles of species for faithful cultural transmission. I suggest a fourth sense begs recognition: fidelity of transmission across many individuals and/or generations. After all, this is what has been argued to be made possible by the episodic fidelity delivered by imitation or other forms of competent copying.

In the limited cases where appropriate archaeological evidence exists for animal culture, nut-cracking using hammer stones has been shown to persist for over 4,000 years in chimpanzees [58] and over 3,000 years in capuchin monkeys [135]. What modern human traditions have displayed more, or even this degree of fidelity, across these recent millennia? Tracing such fidelity in animals in real time is obviously limited by the length of field studies accumulated to date, but diverse chimpanzee traditions identified in the last century have not been reported to alter over periods that for the longest studies exceed five decades. Van Leeuwen [136] reports that alternative mutual grooming customs in four adjacent chimpanzee sanctuary enclosures have remained stable over twelve study years. Even experimentally seeded alternative forms of action such as those in Fig. 5 spread with sufficient fidelity to maintain their arbitrarily instigated differences, and chimpanzees’ discovery of actions that had been seeded in another experimental group were followed by a return to the norms of their own group [99]. Field experiments seeding alternative foraging techniques in different populations of great tits found that these were maintained with high fidelity in a second year despite typical life expectancy of just a few years [24].

What thus seems important for maintaining long-lasting traditions is that cultural transmission processes are of *sufficient fidelity*, rather than the ‘high fidelity’ often proposed. Stability over millennia like in primate stone tools is likely maintained not just by the existence of requisite cognitive transmission processes, but also by the fact that the behaviours concerned deliver resources of significant survival value [137]. This argues against lack of episodic fidelity being the overriding constraints on cumulative culture in animals. The millennia-long fidelity and stability of primate nut-cracking culture, for example, is quite sufficient in principle to permit further cumulative cultural changes if they enhanced fitness. What constrains such ratcheting is the subject of Section 6 below.

5.2. A role for teaching in supporting long-term fidelity of traditions

The persistence of culturally transmitted behaviour may be supported not only by certain forms of social learning from proficient practitioners and associated learning biases [138], but also by actions of such practitioners that actively support transmission, known variously as scaffolding, teaching, or instructed learning [3]. Like culture itself these were once thought unique to humans [3,139]. However when teaching is defined in the functional (rather than intentional) terms proposed by Caro and Hauser [140], requiring only that the actions of one individual aid the learning of another at a cost to itself, a significant catalogue of instances accumulated to merit reviews spanning a diversity of birds, mammals and insects [141,142].

Focusing on the example of meerkats’ first provisioning pups with scorpions with stings removed, and at a later level of skill with sting intact, Thornton and Raihani [142] argue that such structured cultural support is in fact vital for the sustainability of handling and killing this important prey: “repeated interaction with live prey promotes the development of handling skills, so simply observing experienced individuals with prey is unlikely to promote skill acquisition. Pups rarely find mobile prey themselves, so the opportunities for trial and error learning are limited, and incompetent attempts by young pups at handling dangerous prey such as scorpions may be risky. As the probability that pups will acquire hunting skills alone is low, helpers can significantly raise this probability by providing pups with opportunities to learn, so the utility of teaching is high” (p. 1827). Teaching of this kind appears particularly common in predatory species that have to make the leap from being suckled to skilled catching of prey whilst avoiding severe damage to themselves.

Evidence for primates indicates rarer and less structured forms of scaffolding, which Hoppitt et al. [141] suggest is because much foraging is vegetarian and is adequately transmitted by social learning alone during the long childhood of primates. Nevertheless, Musgrave et al. [143] report that tolerant scaffolding, in the form of mothers being prepared to share termite-fishing tools with offspring, is more common in a community that exhibits more complex forms of this skill. There is thus a range of evidence that active contributions by the individual being socially learned from can importantly support transmission of culture and hence the long-term fidelity of such key traditions as those summarised here.

6. So what does limit non-human CCE?

Evidence has accumulated through the present century, and particularly so in recent years, that cumulative culture may occur not only in humans but in a diverse range of behavioural contexts and species [29,36,39,144, for reviews]. The evidence is extremely varied, ranging from rigorously controlled experiments with birds and primates [41,145] to observational field studies of birds, ungulates, cetaceans and primates [[82,146]; [39] for a review]. Transmission chain experimental designs have provided the clearest evidence of progressive cumulative change. Notably, successive replacements of experienced homing pigeons with naïve birds performing repeated homing flights in pairs showed that later pairs in the sequence, by now different to those in earlier phases, nevertheless demonstrated more optimal flight paths [41]. The observational evidence for CCE is naturally more tentative for a variety of reasons, but in some cases data is available to demonstrate cumulative changes over generations, and/or over extended periods that in some cases extend to decades [42–44,46,65].

Debates about the uniqueness of human culture have accordingly now shifted from the argument that cumulative culture exists only in humans to how human and non-human cumulative cultural evolution may differ. Proposals include (i) that non-human cases are limited to reaching some asymptote, such as the fastest route of homing in the pigeon case, whereas human cultures are argued to be open-ended and unlimited [147] and/or (ii) that non-human cases operate only within a single set of natural phenomena (such as navigation in homing), whereas human cumulative culture exploits an expanding set of such phenomena [148]. These more specific ideas now beg empirical evaluation. A limited number of studies have begun to directly probe what may limit nonhuman CCE.

6.1. Experimental probing of the constraints on CCE in chimpanzees

Nobody can dispute that a gigantic gulf exists between human CCE and any CCE operating in non-human animals, yet what limits the latter appears to have been directly empirically probed only in chimpanzees to date. The first experimental test for non-human cumulative cultural learning was in chimpanzees, finding that participants stuck to an initial tool-based technique they had socially learned, rather than 'step up' to a more complex and productive technique modelled by a familiar human [149], whereas children tested later in the same way did assimilate the more complex approach [61]. Interestingly some young chimpanzees unfamiliar with the simple technique did acquire the more complex one, so it is not intrinsically beyond the species, but those learning the simpler technique seemed to become conservatively "stuck" on it, unlike the children. Further variants of this approach similarly found that apes, unlike children, failed to learn from the occasional conspecifics who discovered more complex approaches that gained superior rewards from the task at hand [150–152]. In just one such study was a cumulative step recorded, which, interestingly, occurred only when the innovation was achieved by a pair of individuals acting collectively, and when an ecological challenge was simulated such that existing approaches to the task were thwarted [153,154]. Once the improved innovation emerged, it diffused to others witnessing it.

I suggest that the classic argument, that what constrains CCE in chimpanzees and other animals is a lack of the high fidelity-imitative copying capacity necessary to maintaining traditions long term [3,92] relies largely on reasoning, rather than any empirically demonstrated *causal* linkage. It rests on highlighting two phenomena said to be correlated – differences in both imitation and in CCE – and argues the former is the crucial cause of the latter. Yet any correlation between these two particular phenomena does not necessarily imply that one is the key cause of the other: there exists an enormous diversity of other cognitive differences between human and non-human apes, many likely associated with a tripling in human encephalisation compared to other apes. It seems difficult to maintain the argument that fidelity of transmission is inadequate to main traditions long term, until the next click up in cumulative culture, when some lithic traditions have been sustained for thousands of years [58,135].

Accordingly, some chimpanzee experiments have begun to probe empirically what other factors may constrain individuals in making innovative advances in their behavioural repertoire, or adopting any such advances a group-mate achieves [155,156]. In principle such factors might include limitations in inventive capacities, in physical cognition such as causal understanding, or in motivations to improve on existing actions known to be effective, or assimilating such novel improvements even when witnessed. Exploring these latter possibilities, Davis et al. [155] found that once chimpanzees had learned a long and complex series of repeated combinations of actions to gain a food reward, only a small minority switched to a shorter and more efficient method they witnessed in conspecifics. Such conservatism has emerged as a widespread characteristic in chimpanzees, emerging repeatedly in the small cohort of studies that have presented allied opportunities [149–152]. However when the contrast in efficiency between habitual and novel options was experimentally manipulated to be significantly greater, a number of chimpanzees diverged from this conservatism, switching to the novel and more effective action [155], an effect also found in the study in which small-scale ratcheting up did occur [153]. This suggests that it may take significant pressure of this kind, such as a major ecological change, to stimulate cumulative culture, in chimpanzees at least. The mere opportunity to step up to a superior technique witnessed may not suffice, when a habitual effective option is already in place.

Probing what may underlie the conservatism bias, further experiments revealed that the bias was particularly marked when chimpanzees had spent significant time acquiring a relatively challenging technique, at least part of which needed to be inhibited in order to adopt a novel and now more efficient modified approach [156]. The same individuals were more prepared to inhibit a relatively simple habitual approach, or add a simple modification to a complex habitual method, so as to adopt an improved approach they witnessed. Davis et al. [155,156] therefore suggest that a reluctance to step up from a particularly complex and challenging routine to one that is yet more so may be adaptive because of the potential costs in doing so. Such costs may be instantiated in the form of cognitive and neural demands, and/or in reductions in foraging efficiency as one adaptive peak of performance must be abandoned before a potentially higher one can be scaled – and a lengthy period of practicing a new skill may be required before it is known to deliver a net benefit. It is not suggested that such considerations are necessarily arrived at cognitively, but may instead be dispositions shaped by past successive rounds of natural selection – as discussed next.

6.2. *An evolutionary perspective*

Discussion of contrasts in CCE between human and chimpanzee has focused almost exclusively on proximate differences in hypothesized underlying cultural cognition, as reviewed above. But these should in turn by explicable by reference to the evolutionary histories of the two species since they split from their common ancestry around 7 Ma. We know these histories were enormously different. To a first approximation the human pathway can be characterised as radical, or even revolutionary, the chimpanzee way conservative. Evolving hominins embraced the drastic loss of forest cover in East Africa, becoming bipedal and exploiting a novel savanna-and-woodland, hunting-and-gathering niche that eventually extended to include big game hunting [157–159]. Unprecedented increases in encephalization occurred and technology became sophisticated, particularly that utilized to exploit big game. By contrast, chimpanzees and the other African great apes essentially maintained their arboreal adaptations, thus largely continuing ancestral ways of forest life, without significant enhancements in encephalization.

I submit that these highly contrasting ecological and evolutionary niches may help explain the differences in CCE and cultural cognition. The hominin pathway put a premium on change, the form of which, building on basic ape cultural capacities and inventiveness, was elaborate CCE, particularly technology but also other aspects such as language [160,161], as the means through which a puny ape could compete in savanna and open woodland against "professional predators" like the large sabre-tooth cats hunting big game at the time [159]. The relatively stable, and ancestral niche of forest living great apes, by contrast, will likely have selected for the kind of cultural and other behavioural conservatism described above. Rich and varied ape cultures evolved [15,162], with a modest measure of CCE [46], but change would likely have been slow and cautious by the standards of evolving hominins.

6.3. *Invention, innovation and cumulative invention*

Legare and Nielsen [163] describe the two engines of cultural learning as imitation and innovation. They are surely correct insofar as all cultural traditions require an initial innovation, then socially learned by others: and CCE requires that this process be repeated, as further innovations are added and in turn socially assimilated.

Before focusing here on CCE, a terminological nicety should be recognised. A distinction is being increasingly made by some authors [e.g. [164,12]] between *invention*, defined as the initial creation of a novelty in behaviour or artifact, and *innovation*, when an invention is copied by others to become at least an incipient tradition. I follow this convention here. Other authors continue to include *inventions* in the category of *innovations*, treating the two terms as synonyms.

Consistent with the core message of the present article, other authors have recently argued that an overriding focus on questions of cultural transmission fidelity have been associated with a relative neglect of the role of invention and innovation [165–167]. Perry et al. [165] provide a wide-ranging review of the factors that have been found to influence invention in animals and Bandini and Harrison [168] provide a more focused catalogue of invention by wild and captive chimpanzees. Nishida et al. [169] also catalogued inventions by wild chimpanzees at Mahale, but went further to analyse which of these were incorporated into group life, gaining the status of innovations, and which were not. This was based on retrospective analyses of observational records. By contrast, Perry et al. [170] prospectively and laboriously recorded (perhaps the only scientists to do so) inventions across a ten year period in white-faced capuchin monkeys, and the subset of these that were converted into group life as innovations. In both cases only a relatively small proportion of inventions were incorporated. Of 32 novel behaviours recorded over 25 years in the chimpanzees, only 11 spread significantly to become innovations in the community [169]. Of 187 novel behaviours painstakingly recorded in the capuchins over ten years, about 40 became innovations [170].

Perry et al. [171] offer a comprehensive review of the factors that appear to be effective in converting inventions by animals into community innovations (or conversely, likely to be lost), including characteristics of potential models, learners, dyads, populations and the behaviours themselves. This and all the papers described above in this section make important contributions to the subject of animal culture. However none appears to address the question that I suggest now becomes critical; the extent to which inventions in animals build up on *traditions already in place*, to thus be potentially instrumental in CCE if they turn into innovations.

Perry et al. [165] suggest it may be fruitful to adopt from Boden [172] a three-part dissection of forms of invention into (i) extended *exploration* of an existing behavioural framework; (ii) novel *combination* of existing elements; and (iii) *transformation* of the space of possibilities, for example by adding new elements. The evidence from experiments [41] and long-term observations in the wild [42] that the migratory routes of animals can exemplify CCE may hinge on the extended *exploration* form, where in successive cultural generations, some individuals explore beyond what they acquired culturally from others, and the improved route achieved is then passed on to others in turn, a process plausibly repeating to generate CCE.

The second form, novel combination, could in principle occur within the same behavioural mode, or extend further. Novel combinations of existing elements in the same mode, vocalization, may underlie the cumulative evolution of both birdsong [43] and whale song, including that exemplifying ‘revolutionary’ change [173]. Candidates for novel combinations of different behavioural domains lie most obviously in tool use, where different kinds of tools are combined into ‘toolsets’ [46]. For example, Sugiyama [174] described a chimpanzee first inserting a fashioned leaf-sponge into a tree hole, then using a stick to extract it to drink water from it, an invention that also occurred in the course of an experiment with sanctuary-housed chimpanzees [175]. Vale et al. [153] describe an invention that occurred through some individuals acquiring one key part of a future tool technique (either removing a valve from a tube, or using a tube with valve already removed as a straw to suck up juice), then observing the complementary part in others and combining the two into the whole functional sequence. Others observing the latter acquired the whole sequence, apparently as a package. Note however, that all these instances involve sequential combination of elements, rather than simultaneous combination of elements, as in hafting an axe-head or fitting a string to a bow. Perhaps the latter remains uniquely human.

Identifying “transformation of the space of possibilities” by “adding new elements” will presumably hinge on establishing that novel combinations involve at least one element that is new to the repertoire. This might be consistent with what Derex [148] hypothesises is distinctive about human CCE, namely inventive combination extending to exploit new natural phenomena, as in creating the bow and arrow to supersede thrown spears. Boesch [46] shows that several forms of chimpanzee tool use display different stages of hierarchical complexity consistent with this, but we lack a historical record that demonstrates this is the result of step-wise CCE. Achieving this may depend on cataloguing not only all observed inventions in a wild population of animals over long periods as Perry et al. [170] have done, but attending in particular to episodes in which combinations involving newly invented elements build on prior culturally transmitted techniques. This remains a tall order.

7. Conclusions

The ZLS hypothesis [50,51] can be regarded as a more specific offshoot of its ‘parent’, ICH [3,92]. I have critiqued both, but that concerning the ZLS concept and research programme merited greater severity. I highlighted logical incoherence in its core hypothesis (3.1), and the failure to deal with the fact that all cultural traditions require initial innovation by one or more individuals (3.2), together with a suite of problems in the realities of empirical testing and other aspects of investigation (3.3-3.5). I urge that researchers should therefore be wary of being led along what may be an ultimately sterile blind alley.

The ICH is different. The broad proposition that human cultural transmission can often be particularly high fidelity compared to that common in chimpanzees or other species is supported by much empirical evidence, including some of my own comparative studies [96,176,177]. What I take issue with are assertions that chimpanzees (and some other nonhuman species) *cannot* and *do not* imitate (whether limited to bodily imitation or imitation conceived more broadly), that they *cannot* and *do not* copy what others are observed to do (including new invented actions), and that for these reasons traditions cannot be maintained with any fidelity long term, to allow CCE to occur.

In this article I have reviewed evidence that none of these is the case. My analysis converges with other recent perspectives perceiving a misleading over-emphasis on social transmission deficits at the expense of other factors contributing to interspecific differences in cultural evolution and CCE [165–167,171,178]. None of this is to dispute that individual learning processes can also play a big part in cultural acquisition processes, including iterative alternation of observational learning and practice of what has been observed [179].

Many of the studies I have relied on in my analysis illustrate more fruitful research pathways, already instigated across a diversity of vertebrate and invertebrate taxa, and with promise for further significant contributions to the field [180], contrasting with those I critique. Powerful methodologies that underlie such productivity include two-action methods to rigorously test for the copying of alternative forms of action, transmission chain and other diffusion experiments of several kinds to investigate the spread and fidelity of traditions [9,24,27,106], and experiments designed explicitly to offer opportunities for CCE, testing the conditions for both its emergence and limitation [149–154,175]. By contrast in perhaps only a single study have any of the demonstrably fruitful approaches listed in this paragraph been applied by the principal proponents of the ZLS or ICH [181].

Some of the latter authors have argued that baseline or other control conditions lacking a model are essential, yet too often lacking [182]. My final point is that this depends on the question at hand. If the question is about the relative roles of social versus individual learning, then such controls will naturally play a critical role and many have been done. However if interest instead focuses on processes of cultural transmission, especially concerning a role for copying forms of action, then a two action methodology alone, without a no-model condition, provides an entirely adequate test for such transmission. Where an asocial control test is added, one that reveals rare success, rather than no success, will be more representative of culture under natural conditions, where every new tradition, whether one built cumulatively or not, requires an inventor to first create it.

Declaration of competing interest

The author declares that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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