

Leveling the Playing Field in Studying Cumulative Cultural Evolution: Conceptual and Methodological Advances in Nonhuman Animal Research

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Cumulative cultural evolution (CCE), the improvement of cultural traits over generations via social transmission, is widely believed to be unique to humans. The capacity to build upon others' knowledge, technologies, and skills has produced the most diverse and sophisticated technological repertoire in the animal kingdom. Yet, inconsistency in both the definitions and criteria used to determine CCE and the methodology used to examine it across studies may be hindering our ability to determine which aspects are unique to humans. Issues regarding how improvement is defined and measured and whether some criteria are empirically testable are of increasing concern to the field. In this article, we critically assess the progress made in the field and current points of debate from conceptual and methodological perspectives. We discuss how inconsistency in definitions is detrimental to our ability to document potential evidence of CCE to nonhuman animals. We build on Mesoudi and Thornton's (2018) recently described core and extended CCE criteria to make specific recommendations about, from a comparative lens, which criteria should be used as evidence of CCE. We evaluate existing data from both wild and captive studies of nonhuman animals using these suggestions. We finish by discussing issues currently faced by researchers studying CCE in nonhuman animals, particularly nonhuman primates, and provide suggestions that may overcome these concerns and move the field forward.

Keywords: comparative psychology, cumulative cultural evolution, innovation, social learning, nonhuman animals

Over recent decades, the topic of cumulative cultural evolution (CCE)—in which cycles of innovation and social learning lead to adaptive modifications accumulating over historical time—has

become a focal topic in biological and social sciences (Caldwell & Millen, 2008; Dean et al., 2014; Legare, 2017; Mesoudi & Thornton, 2018; Tennie et al., 2009). CCE is key to the sophisticated technologies, customs, and knowledge that pervade our lives and is the reason humans have such developments as complex social institutions, rituals, biomedicine, agriculture, and literature (Boyd & Richerson, 1985; Henrich, 2015; Legare & Nielsen, 2020; Muthukrishna & Henrich, 2016). Computers, for example, are not the invention of any one individual but are the product of centuries of cumulative cultural improvement; they have evolved from steam-based analytical engines in the early 1800s to Alan Turing's seminal machine capable of algorithmic logic, to large, single-circuit digital desktops computers, all of which are products of building upon others' output (with hundreds of iterations in between), paving the way for the lightweight and computationally powerful laptops we use today. Likewise, over generations, horticultural societies have developed sophisticated processing techniques to process otherwise-toxic foods, such as cycads and cassava, to provide new sources of food (Beck, 1992; Henrich & Henrich, 2010; Wilson & Dufour, 2002). Researchers have extensively examined what underpins CCE, its evolutionary origins, and whether it exists outside of humans, driven by the aim of understanding the success

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of our species (reviewed in Caldwell et al., 2020; Dean et al., 2014; Tennie et al., 2009; Vale, Carr, et al., 2017).

CCE has affected all human cultures across a diverse set of domains, including knowledge of foraging subsistence-oriented societies (Reyes-García et al., 2016; Salali et al., 2016), tool complexity in Tasmania (Henrich, 2004), the hunting techniques of the Central Inuit in the Canadian Arctic (Boyd et al., 2013), the structure and transmissibility of language (Kirby et al., 2008) and folktales (Acerbi et al., 2017; Tehrani, 2013), and religious practices (Norenzayan & Gervais, 2011). Key to CCE is the social dissemination of improved skills, knowledge, behaviors, and artifacts within groups that lead to adaptive changes. Many nonhuman animal species are capable of social learning (learning by directly observing other organisms or the by-products of their actions; Heyes, 1994), and some even show cultural traditions—group typical behavior that is socially transmitted (Laland & Janik, 2006). Population-specific foraging, tool use, and social and communicative behaviors across taxa such as apes, monkeys, birds, and cetaceans are a result of the social transmission of these behaviors within groups (Allen et al., 2013; Aplin et al., 2015; Gruber et al., 2015; van Schaik, 2003; Whitehead & Rendell, 2014; Whiten, 2019; Whiten et al., 1999). Yet, concrete evidence for cultural change in a way that *cumulatively improves* existing skillsets over time outside of humans remains elusive (Caldwell, 2020; Mesoudi & Thornton, 2018). In particular, it may be challenging to show adaptive change over historical time in nonhuman species, much less in experimental contexts, because their cultural traditions either lack artifacts (i.e., are behavioral) or show less apparent change. However, although no other species have anything close to our sophisticated technologies, symbolic languages, and institutions, as we present here, more basic forms of cultural improvement may be present across a range of taxa (Wilks et al., 2021). Understanding these will help us understand the evolutionary history of humans' impressive capacity for cumulative culture.

Indeed, conclusions about the uniqueness of cumulative culture in humans may be precluded by a lack of consistency in both the definitions and criteria used to determine CCE and the methodology used to examine it across different animal species. Concerns regarding how improvement is defined, whether it is measured the same way across studies, and whether some criteria are empirically testable are of increasing interest to many researchers (Caldwell et al., 2020; Mesoudi & Thornton, 2018; Miton & Charbonneau, 2018; Reindl et al., 2020; Schofield et al., 2018). After all, inconsistent use of definitions means studies are not comparable, making it difficult to assess how CCE may differ across contexts, much less across different species. The latter of these is essential to understand the evolutionary history of CCE and how it came to be such a dominant force in humans.

The primary goal of this article is to provide a critical assessment of conceptual and methodological advances within the field of CCE with respect to nonhuman animals. We begin with a review of how definitions to assess CCE have evolved, particularly concerning current debates surrounding scientific parsimony. After considering how these debates and developments have affected our ability to attribute CCE to nonhuman animals, we make specific recommendations about which criteria should be used. We then use our recommended criteria to assess the existing evidence

from both wild and captive studies of nonhuman animals before discussing what research is needed going forward to advance the field. Throughout the article, we focus largely on nonhuman primates because, based on their phylogenetic and cultural proximity to humans, they have been the focus of the majority of nonhuman animal CCE research—particularly chimpanzees (Whiten, 2019). We also argue that the field must continue to expand beyond primates, however, and thus, where relevant, we include literature from nonprimates.

The Evolution of Definitions and Assessment of Cumulative Cultural Evolution

Early characterizations of cultural improvement were relatively broad, focusing on the “ratchet effect”—a process whereby the complexity of cultural traits (e.g., skills, knowledge, technology, and customs that are transmitted socially within communities) is improved through generations of innovations and their subsequent social transmission (Tomasello et al., 1993). By this definition, cycles of modifications to, and ensuing social dissemination of, cultural traits allow the ratcheting of knowledge with little or no “backward slippage” (loss of knowledge or reversion to previous, less efficient behavior). These cycles were suggested to culminate in products that no single individual could invent from scratch within their lifetime (Boyd & Richerson, 1996; Dean et al., 2012; 2014). The attribution of human uniqueness of CCE was based on the assumption that only humans possess the required capacity for high-fidelity social learning to faithfully maintain improvements over time and prevent backward slippage. This view continues to be contentious, however, because (a) similarly high-fidelity social learning may also be present in some nonhuman animals (Boesch et al., 2020; Horner & Whiten, 2005; Loretto et al., 2020; Musgrave et al., 2020; Whiten et al., 1996, 2009), and (b) experimental research with humans has shown that cumulative technological improvement can occur without high-fidelity social learning (Caldwell & Millen, 2009; Zwirner & Thornton, 2015; although see Wasieleski, 2014).

A large body of subsequent research has since highlighted theoretical and experimental challenges to these early definitions (Caldwell et al., 2020; Dean et al., 2014; Haidle & Schlaudt, 2020; Mesoudi & Thornton, 2018; Miton & Charbonneau, 2018; Reindl et al., 2020; Schofield et al., 2018). For instance, although almost all researchers agree that CCE requires cultural traits to show improvement over time through a process of building upon previous generations (Caldwell, 2020; Davis et al., 2016; Dean et al., 2014; Legare, 2017; Mesoudi & Thornton, 2018; Sasaki & Biro, 2017; Tennie et al., 2009; Weston & Jackson, 2018; Whiten, 2017a), improvement is not always defined or measured consistently. From an evolutionary perspective, improvement should represent adaptive modifications over historical time (Boyd et al., 2011; Derex & Mesoudi, 2020; Fay et al., 2019; Henrich, 2004; 2015; Winters, 2019), yet experiments only measure short-term improvement rather than long-term adaptive changes. There is thus a disconnect between what, globally, we aim to know about cumulative improvement and what we can measure in laboratory settings.

Experimentally, improvement is typically described as an increase in the complexity or efficiency of a behavior (Dean et al., 2014), but these constructs themselves are inconsistently measured

(Schofield et al., 2018). Complexity, for example, can refer to the number of behavioral steps or techno-units required to achieve a goal (Boesch et al., 2019; Davis et al., 2019), differences in the hierarchical structure of behaviors (Boesch et al., 2019; Byrne & Byrne, 1993), or overall level of difficulty (Caldwell et al., 2018). Efficiency can be measured in terms of speed, learnability, a reduction of behavioral steps, calorie intake, convenience, or security (Davis et al., 2016; Schofield et al., 2018; Stewart et al., 2007; Yamamoto et al., 2013). Given that studies differ substantially in how they measure these constructs, we suggest that clearly stating units of measurements will provide clarity, help to refine cross-study evaluations, and allow a clearer assessment of the impact of improvement on other outcomes, such as adaptive value, payoffs, or productivity (Schofield et al., 2018).

A broader conceptual issue is that definitions of CCE may refer to both cultural processes (cumulative improvement) or cultural products (behavioral outputs; Reindl et al., 2020). Process-based definitions, as defined by Reindl and colleagues, require improvements in complexity or efficiency over generations of social transmissions but are not concerned with the actual quantity of complexity or efficiency of the *final* product (McGuigan et al., 2017; Mesoudi & Thornton, 2018). Product-based definitions, conversely, define the improved complexity/efficiency as that which goes beyond what a naïve individual could invent within their lifetime (Boyd & Richerson, 1996; Reindl et al., 2017, 2020; Tennie et al., 2016). Researchers generally elect for either process- or product-based definitions, and this has significant consequences for the underlying cognitive mechanisms involved (Rawlings & Legare, 2021), the extent to which CCE is uniquely human or not, and even whether different cohorts of the same species share CCE (e.g., children, adults, or both; Reindl et al., 2020). Using different criteria also moves the goalposts concerning what is classified as CCE and hinders our capacity to make fair cross-species comparisons and thus to fully understand the evolutionary origins of CCE. These issues also present important philosophical questions regarding comparisons of CCE behavior between humans and nonhuman animals. To what degree should researchers define phenomena such as CCE based on their experimental tractability (i.e., process-based criteria)? Should we limit definitions to what is testable? Study designs hinge on such questions; without tethering our definitions to empiricism, we cannot scientifically evaluate them. Yet, capturing a phenomenon based on what is possible to empirically examine risks overlooking very important aspects of the behavior (i.e., product-based criteria).

Further, the use of the criterion that CCE leads to traits (e.g., adaptive behaviors, skills, or artifacts) beyond which an individual can invent within their lifetime is increasingly being questioned because it is impossible to experimentally examine in long-lived species such as humans and apes (Caldwell et al., 2016; Mesoudi & Thornton, 2018; Miton & Charbonneau, 2018; Schofield et al., 2018). This criterion emphasizes the power of collective knowledge and provides a broader framework for CCE (in addition to measures of improvements in complexity and efficiency). Experiments typically reduce generations or lifetimes to a matter of minutes or hours and thus cannot adequately or ethically assess whether a solitary individual can invent a product of CCE in their lifetime (Mesoudi & Thornton, 2018; Miton & Charbonneau, 2018).

In an attempt to overcome some of the definitional discrepancies just outlined, Mesoudi and Thornton (2018) recently described both core and extended criteria for attributing CCE to a population (which can be applied to assess CCE for any behavior found in a given population of any animal species). The core criteria, representing the minimum requirements for a population to display CCE, include (a) a change in behavior (or product of behavior, such as an artifact), typically due to asocial learning, followed by (b) the transfer via social learning of that novel or modified behavior to other individuals or groups, where (c) the learned behavior causes a performance improvement, which is a proxy of genetic and/or cultural fitness, with (d) the previous three steps repeated in a manner that generates sequential improvement over time. According to this account, Criteria a and b equate to cultural change (i.e., the transmission of innovations); the addition of Criterion c would be evidence of cultural evolution (where the innovation causes improvement); and to distinguish cultural evolution from cumulative cultural evolution, Criterion d is required (where this improvement repeats over time). The extended criteria, which may or may not be present and may be scaffolded by different sociocognitive mechanisms than the core criteria, include (a) multiple functionally dependent cultural traits (e.g., when new innovations are contingent upon previous ones), (b) diversification into multiple lineages (e.g., different types of projectile tools for hunting), (c) recombination across lineages (combining cultural traits to develop new ones), (d) cultural exaptation (i.e., a change in a cultural trait's function), and (e) cultural niche construction (i.e., where cultural traits impact the selective environments of other biological or cultural traits). Criteria such as these provide a valuable metric with which to classify candidate behaviors as evidence of CCE or not.

Here we build upon these recent criteria proposed by Mesoudi and Thornton (2018) to define CCE from a comparative perspective. From a practical standpoint, we believe a criterion needs to be empirically tractable, and so we focus on criteria that can be assessed and experimentally tested in nonhuman species. To this end, the CCE criteria we think are most suitable for nonhuman animal testing (with particular consideration of nonhuman primates) would be core Criteria a–c (the transmission [Criterion b] of a new behavior [Criterion a] that causes performance improvements [Criterion c]). We further suggest that improvements should be those that surpass what an individual can accomplish when exposed to the same conditions (Criterion d), although we recognize that determining what is needed for conditions to be the same can be difficult. This distinguishes cases of cultural change and cultural accumulation (where behaviors are added to repertoires, but they are not more complex; Dean et al., 2014) from CCE, which requires measurable improvement. It is important to note that although prior cultural knowledge can influence the inventive capacities of individuals, testing whether group behaviors exceed individual achievements provides a useful benchmark to distinguish CCE from cultural evolution. This means, in our definition, CCE could be attributed to novel behaviors that are improvements upon previous versions (beyond an individual's abilities) and that are transmitted to others.

We propose that an extended criterion should include that these steps are repeated over generations (which is core Criterion d from Mesoudi & Thornton, 2018) because for some animal species, including nonhuman primates, assessing generational improvements

is highly difficult (Caldwell et al., 2020). In captivity, generational transmission-chain experiments (where information is passed along chains of individuals and improvement is measured) are logistically problematic, requiring access to sufficient sample sizes and facilities that permit this type of testing (issues discussed in detail later). Obtaining generational data from wild populations requires longitudinal observations, which is equally, or more, difficult. Thus, although we agree that evidence of invention and social spread leading to improvement (Criteria a–c) being repeated over time would be optimal, it is not always feasible to measure. Therefore, although we find the use of such criteria extremely valuable for classifying behaviors as evidence of CCE, we suggest that a more inclusive definition, applicable to diverse taxa, may also help further our understanding of the evolution of CCE. Using these criteria, we now present and assess evidence of CCE in nonhuman primates and, where applicable, other species, based on studies of wild and captive populations (see Table 1).

Cumulative Culture in Nonhuman Animals: Evidence From Wild and Captive Populations

As evidence for culture in nonhuman animals grows (Aplin et al., 2015; Gruber et al., 2019; Laland & Galef, 2009; Whiten, 2017b, 2021; Whiten et al., 1999), researchers are examining whether nonhumans are capable of CCE. Various approaches have been developed, from documenting complex traits in wild populations to sifting through historical data sets, to experimentally manipulating behavioral complexity and efficiency in laboratory-controlled settings.

CCE in Nonhuman Primates: Evidence From the Wild

Reports of group-level traditions in wild nonhuman primate populations, similar to human culture, are now well documented (see Boesch et al. [2019], McGrew [1992], and Whiten et al. [1999] for chimpanzees [*Pan troglodytes*]; Hohmann and Fruth [2003] for bonobos [*Pan paniscus*]; Perry [2011] for capuchins [genus *Cebus*]; Robbins et al. [2016] for gorillas [*Gorilla gorilla*]; van Schaik et al. [2003] for orangutans [*Pongo*]). Some of these traditions, such as chimpanzee nut-cracking, vary in their complexity across populations, leading some to suggest they have undergone successive refinements and that they therefore represent examples of CCE (Boesch, 2003).

Perhaps the most famous traditions include chimpanzees' community-specific styles of constructing and using tools during extractive foraging that are not easily attributed to ecological or genetic dissimilarities. This strengthens the conclusion that these inventions (Criterion a) spread by social learning (Criterion b). Taking nut-cracking as one example, chimpanzees in Bossou, Guinea, and Taï Forest, Côte d'Ivoire (Whiten et al., 2001) display sophisticated procedures of using several tools to open the hard-shelled nuts found in their habitats (see also Coelho et al. [2015] and Eshchar et al. [2016] for similar cases of nut-cracking in capuchin monkeys). These two populations use wooden and stone hammers in conjunction with an anvil and, more rarely, with a third component of a stone to stabilize the anvil (Boesch et al., 2019; Luncz & Boesch, 2014; Matsuzawa, 1994; Sugiyama, 1997; Sugiyama & Koman, 1979). Researchers have suggested that composite (two or more tools used together to achieve a goal; here,

hammers and anvils) and compound tool use (combining elements to make a single unit; here, the wedge added to the anvil) represent elaborations of the simpler percussive act of hitting (soft) shells with one's arm, or a single tool, perhaps indicative of some form of CCE (Boesch, 2003). Neighboring groups' specificity in their material selections also has consequences for the efficiency of these cultural traits, as measured by foraging speed and the number of actions required to crack open nuts (Luncz et al., 2018). However, although community differences in complexity and efficiency may indicate trait modification, there is a lack of evidence of directionality to confirm that simple trait variants preceded more sophisticated ones. Without such evidence, it is difficult to assert that the behavior has undergone beneficial modifications (uncertainty of Criterion c).

A further concern here is whether the learned behaviors are beyond what may be invented by a solitary chimpanzee in comparable conditions (Criterion d). This has also proven difficult to test experimentally. Chimpanzees in the wild begin to crack nuts successfully by approximately 3.5 years of age (Inoue-Nakamura & Matsuzawa, 1997) and master the behavior when they are 5–6 years old (Estienne et al., 2019). Moreover, there appears to be a sensitive period of between 3.5 and 10 years of age during which they can develop the skill (Biro et al., 2003; Inoue-Nakamura & Matsuzawa, 1997; Matsuzawa, 1994). Both the extended learning period and the limited age during which learning appears to occur make it difficult to study in laboratory settings. A recent study found no evidence that 13 naïve captive chimpanzees, aged 10–52, would spontaneously crack nuts with tools after 92 hr of practice (Neadle et al., 2020), which may suggest it is not easily invented. However, the authors also reported no evidence that chimpanzees could socially learn this behavior, perhaps suggesting that the chimpanzees either received too little exposure or were past the sensitive period (Neadle et al., 2020). Indeed, in a group of two 6-year-old chimpanzees, individuals 3 years and over learned to crack open nuts on a stone anvil within days after observing con- and hetero-specific demonstrations (Marshall-Pescini & Whiten, 2008b). This contrasted an age-matched control group that showed no such learning until they received social demonstrations (Marshall-Pescini & Whiten, 2008b), highlighting the importance of social learning in the development of nut-cracking technologies during early chimpanzee ontogeny.

Another case for CCE in chimpanzees has been made for their termite fishing behaviors. In a large-scale study, Boesch et al. (2020) collated data from multiple chimpanzee communities, documenting a detailed analysis of the technical elements they use to access termites. Overall, there was impressive diversity in the techniques employed, with 38 different elements involved, 30 of which could not easily be explained by community ecological conditions. Some newly observed community-specific elements (*circumstantial* evidence of inventions, Criterion a), such as orientation, for instance, by leaning on their elbow or lying on their side, were suggested to have spread by social learning (Criterion b). Groups further differed in the specific combinations of elements they used, some of which include tool modifications (e.g., making of brush-tipped probes) that could lead to improvements in behavioral efficiency (Sanz et al., 2009). Such community-specificity in the complexity of the behavioral sequences used to extract termites, as with the nut-cracking example, resemble cumulative additions to behaviors (see Boesch et al., 2020; Dean et

Table 1
Studies of Potential Cumulative Cultural Evolution in Nonhuman Animals Against Our Proposed Criteria

Study	Species	Observed behavior	Wild/captive/field experiment	Core criteria				Extended criteria	
				Invention (Criterion a)	Social transmission (Criterion b)	Measurable improvement through Criteria a and b	Exceeds individuals' discoveries (Criterion d)	Repeated over generations	
Allen et al. (2018)	Humpback whales (<i>Megaptera novaeangliae</i>)	Song structure	Wild	✓	C—Probable but no direct evidence	✓—Cycles of increases and decreases in song complexity	x	✓	
Boesch et al. (2020)	Chimpanzees (<i>Pan troglodytes</i>)	Termite fishing	Wild	C—Circumstantial evidence through newly documented behavioral elements	C—Probable but no direct evidence	C—Probable but no direct evidence	x		C—Circumstantial evidence documenting behavior in multiple generations
Chimento et al. (2021)	Great tits (<i>Parus major</i>)	Puzzle box: two levels of efficiency	Captive (except children)	✓	✓	✓	x	✓	
Claidière et al. (2014)	Baboons (<i>Papio papio</i>)	Memorizing patterns on touchscreens	Captive (except children)	✓—Change through transmission error	✓—No social interaction but met social learning definition of the products of others' behavior	✓—If invention is a group process and social learning can be indirect	✓	✓	
Davis et al. (2016)	Chimpanzees (<i>Pan troglodytes</i>)	Puzzle box: two levels of increasing efficiency	Captive (except children)	Invention model seeded	✓	✓	x	x	
Davis et al. (2019), Study 2.1	Chimpanzees (<i>Pan troglodytes</i>)	Puzzle box: two levels of increasing complexity	Captive (except children)	Invention model seeded	✓	✓	x	x	
Dean et al. (2012)	Children, chimpanzees, and capuchins (<i>Homo sapiens</i> , <i>Pan troglodytes</i> , <i>Cebus apella</i>)	Puzzle box: three levels of increasing complexity	Captive (except children)	✓	✓—But children only	✓—But only children reached hardest level	x—Reindl et al. (2020)	x	
Fehér et al. (2009)	Zebra finches (<i>Taeniopygia guttata</i>)	Song structure	Captive (except children)	✓	✓	C—Change toward wild-type song; unknown if change represents improvement	✓	✓	
Garland et al. (2011)	Humpback whales (<i>Megaptera novaeangliae</i>)	Song structure	Wild	C—Indirect evidence through changing song	✓	C—Unknown if changes represent improvement (although Allen et al. [2018] document changes in complexity)	x	✓	✓Repeated change over 11 years

(table continues)

Table 1 (continued)

Study	Species	Observed behavior	Wild/captive/field experiment	Invention (Criterion a)	Core criteria			Extended criteria
					Social transmission (Criterion b)	Measurable improvement through Criteria a and b	Exceeds individuals' discoveries (Criterion d)	
Garland et al. (2017)	Humpback whales (<i>Megaptera novaeangliae</i>)	Song structure	Wild	✓	✓	x	x	x
Hunt and Gray (2003)	New Caledonian crows (<i>Corvus moneduloides</i>)	Tool use	Wild		C—Indirect evidence of diverse tools	C—Probable but no direct evidence	C—Probable but no direct evidence	x
Jesmer et al. (2018)	Bighorn sheep (<i>Ovis canadensis</i>)	Migration routes	Wild (historical data)	x	✓	✓	✓	C—Circumstantial evidence documenting behavior in multiple generations
Loukola et al. (2017)	Bumblebees (<i>Bombus</i> spp.)	Transporting objects	Captive (except children)	✓	✓	✓	x	x
Luncz et al. (2018)	Chimpanzees (<i>Pan troglodytes</i>)	Nut-cracking	Wild	C—Original invention not observed	C—Indirect evidence of variations between neighboring groups	x—Differences in efficiency documented for neighboring groups but no improvements to a single trait	x—But some evidence that this behavior is not reinvented by naive chimpanzees (Bandini & Tennie, 2020)	x—But evidence is reported elsewhere (e.g., Mercader et al., 2007)
Luther and Derryberry (2012)	White-crowned sparrow (<i>Zonotrichia leucophrys</i>)	Song frequency	Wild	✓	C—Probable but no direct evidence	✓	x	C—Circumstantial evidence documenting behavior in multiple generations
Marshall-Pescini and Whiten (2008b)	Chimpanzees (<i>Pan troglodytes</i>)	Nut-cracking	Captive (except children)	Invention model seeded and one chimpanzee showed the behavior, thought to be due to past experience	✓	x	x	x
Marshall-Pescini and Whiten (2008a)	Chimpanzees (<i>Pan troglodytes</i>)	Puzzle box: two levels of increasing complexity	Captive (except children)	✓	✓—Simple behavior only	x	x	x
Perry et al. (2003)	Capuchin monkeys (<i>Cebus apella</i>)	Social rituals	Wild	✓	✓	x	x	x
Price et al. (2009)	Chimpanzees (<i>Pan troglodytes</i>)	Tool-combining task to reach rewards	Captive (except children)	Invention model seeded and invention in controls	✓	✓	x—Discovered by individuals with no social demonstrations	x
			Wild	x	✓	✓	x	x

(table continues)

Table 1 (continued)

Study	Species	Observed behavior	Wild/captive/field experiment	Invention (Criterion a)	Core criteria			Extended criteria
					Social transmission (Criterion b)	Measurable improvement through Criteria a and b	Exceeds individuals' discoveries (Criterion d)	
Sanz et al. (2009)	Chimpanzees (<i>Pan troglodytes</i>)	Chimpanzee termite fishing			C—Probable but no direct evidence			
Sasaki and Biro (2017)	Homing pigeons (<i>Columba livia</i>)	Homing routes	Field experiment	✓	✓	✓	✓	✓
Schofield et al. (2018)	Japanese macaques (<i>Macaca fuscata</i>)	Food-washing behaviors	Wild (historical data)	✓	C—Probable but no direct evidence	✓	x	✓
Vale et al. (2021)	Chimpanzees (<i>Pan troglodytes</i>)	Tool use and tool modification task	Captive (except children)	✓	C—Probable transmission of simple but not complex techniques	x	x	x
Vale, Carr, et al. (2017)	Chimpanzees (<i>Pan troglodytes</i>)	Complex tool behavioral sequence	Captive (except children)	Invention model seeded and invention in a nonseeded group	✓	✓	✓—But partial discovery in asocial control individual	x
Williams et al. (2013)	Savannah sparrows (<i>Passerculus</i>)	<i>sandwichiensis</i>	Song segments	Wild	x	✓	✓	x
Yamamoto et al. (2013)	Chimpanzees (<i>Pan troglodytes</i>)	Extracting juice from container	Captive (except children)	✓	✓	✓	x	x

Note. ✓ = meeting the criterion; x = failing to meet criterion; and C = circumstantial or indirect evidence of meeting the given criterion.

al., 2014). Without observation of their inception and development over time, however, we cannot be sure that these behaviors evolved in complexity or efficiency (Boesch et al., 2020; although see Sanz et al., 2009; Criterion c), nor that they exceed individuals' ability to invent (Criterion d). Although individual discovery of the exact community-specific styles of termite fishing (involving numerous behavioral elements) seems improbable, we cannot rule this out with current data.

To circumvent speculation over the developmental course of recently observed traits, researchers have examined long-term data sets spanning multiple generations (thus meeting our extended criteria). Schofield et al. (2018) reviewed over 60 years of observations of Japanese macaques' (*Macaca fuscata*) food-washing behaviors. This data set included the first instance of sweet potato washing followed by wheat washing (Criterion a), allowing researchers to track the spread (Criterion b) and progressive enhancements to these behaviors since their inception (Criterion c). Various modifications were observed that might represent cumulative increases in complexity and efficiency (Schofield et al., 2018). Similar longitudinal observations have been conducted with white-faced capuchins (Perry, 2011; Perry et al., 2003, 2017), tracing the development and diffusion of a number of social conventions, but there is a question about whether they have improved over time, and their reinvention suggests they do not surpass what individuals can invent for themselves (Dean et al., 2014). Tracing innovations and behavioral change across generations is extremely time intensive but promises to shed light on the cumulative cultural abilities of other species. Although there remains a question over the role that social learning (Criterion b) plays in the transmission of behaviors such as these because it is not directly observed (Caldwell et al., 2020; Fiore et al., 2020), we hope that continued observations of wild communities' inventions and their spread will shed more light on whether CCE is shared with other animals.

CCE in Nonhuman Primates: Experimental Evidence

To our knowledge, it was not until 2008 that the first experiment was conducted to explicitly test whether chimpanzees display CCE. Marshall-Pescini and Whiten (2008a) presented 11 young chimpanzees with a honey-dipping task that could be solved using the relatively simple act of dipping a tool into a contraption to gain honey or a more complex action of first removing a bolt before leveraging open a lid to reveal a large compartment of honey and peanuts. Overall, five chimpanzees demonstrated the ability to dip for honey, either personally discovering the action during baseline trials (Criterion a) or acquiring it following social demonstrations (Criterion b). The more complex action, by contrast, was not acquired, despite participants receiving a substantial number of demonstrations (not meeting Criterion c). This was not because the more optimal behavior was too challenging for them—task-naïve chimpanzees easily discovered the complex act through personal exploration (not meeting Criterion d). The authors thus raised the proposition that the chimpanzees displayed behavioral conservatism, such that their known behavior (“dipping”) interfered with the adoption of the more productive alternative that was otherwise in their ability to acquire (Marshall-Pescini & Whiten, 2008a)—a hypothesis that inspired further studies (which we discuss later in the article).

The next study of CCE in nonhumans was by Dean et al. (2012), who took a comparative approach on a larger scale, comparing the performance of group-housed chimpanzees and capuchins to nursery-aged children. Experiments that make such cross-species comparisons are particularly important because they can identify trait similarities and differences across species and shed light on their evolutionary histories (Liebal & Haun, 2012). All three species were posed an extractive foraging task similar to that in Marshall-Pescini and Whiten (2008a), but these tasks had three sequential and increasingly difficult steps that revealed a progressively valuable reward (Dean et al., 2012). Whereas chimpanzees and capuchins had difficulty in reaching complex task solutions, either by individually discovering them or by learning socially from a proficient conspecific, many of the children quickly solved the task. Children also displayed several sociocognitive processes related to their task success that were largely absent in the other primates, including sharing reward (altruistic resource donation) and knowledge (via teaching), as well as copying the actions of group members in their group (imitation). High-fidelity social learning mechanisms, including imitation and teaching, support the transmission of particularly complex knowledge or cultural traits, for which other mechanisms, such as trying to re-create products through backward engineering (emulation), may be insufficient (Caldwell et al., 2018; Morgan et al., 2015) and are thus important contributors to the level of complexity a species can reach. This suite of psychological processes was hence suggested to be key in supporting children's ability to transition to more sophisticated and rewarding techniques, enabling them to outperform the nonhuman participants (Legare, 2019).

A limitation of this study was the absence of an asocial control to ensure that individuals could not independently solve the task (Criterion d). To address this, a new population of children was tested on the same task previously presented to groups to see if they could solve the puzzle box through personal exploration (Reindl et al., 2020). Notably, 9 out of 35 children discovered all three task levels without social demonstrations. Children in this study failed to meet the authors' product-orientated definition of cumulative cultural evolution, which requires the behavioral products of group-tested participants to exceed those of individuals (Reindl et al., 2020; Criterion d). Instead, the authors proposed that Dean et al. (2012) had shown elementary cumulative cultural learning that was process orientated, involving change through invention and social learning but without requiring the end result (task level) to surpass what individuals could invent.

Transmission Chains, Replacement Methods, and Open Diffusions

Subsequent studies have experimentally examined CCE in other animals, including birds (Sasaki & Biro, 2017) and baboons (Claidière et al., 2014), using transmission chains to closed-group, open-diffusion types of tasks (described later in the article) to reveal evidence for cultural improvement. Transmission-chain designs involve one participant, or “model,” providing task-relevant social information to a naïve observer before they perform the same task, with the latter then acting as the model to a new individual in the chain, and so on (Whiten & Mesoudi, 2008). Using this method, baboons were given a pattern-recognition task in which the output of the previous participant formed the stimuli

for the following participant in the chain, and so on (Claidière et al., 2014; also see Saldana et al., 2019). Over time, pattern reproduction improved (increased performance; Criterion c) because there emerged structure in the lineages and across “generations,” similar to how human languages evolve (Kirby et al., 2008). Importantly, repeated exposure to one’s own learning output did not yield the same level of change, suggesting that chains comprising different individuals were responsible for improving the learnability of the task (meeting Criterion d).

Similar improvements across transmission chains have been reported in homing pigeons (*Columba livia domestica*), where the homing routes of birds later in chains were more efficient than earlier “generations” and solo individuals (Sasaki & Biro, 2017). “Generational” change was explored by first pairing a bird with an established homing route with a naïve flight partner. Once this naïve partner had flown with their partner, they became the experienced participant paired with the next naïve subject in the chain, and this process continued until five successive generations were formed. Birds in the transmission chain showed measurable improvements in their routes, such that the fifth generation’s routes were 1.2 km shorter than those of the first generation (meeting the extended criterion of generational improvements). This improvement over time was also more pronounced than for solo birds repeating the same number of flights, which produced only a .05-km reduction in their route—therefore meeting Criterion d.

Improvements in behavioral efficiency have also recently been documented in great tits (*Parus major*) using the “replacement” method. This method is similar to transmission chains, except each generation is a group of individuals instead of a dyad (Chimento et al., 2021). Here, birds could gain a reward by either pushing open a door in a demonstrated but inefficient direction, or they could innovate the efficient, quicker alternative by pushing the door from the opposite side. For birds that were in the “static” control condition, repeatedly testing the same groups of birds, the efficient behavior was discovered (easily invented; thus not meeting Criterion d) but was not widely adopted. For the birds in the “turn-over” condition, repeatedly replacing two of the six birds in each “generation” with naïve ones, the efficient alternative was not just invented (Criterion a) but also widely adopted (social transmission [Criterion b] and improvement [Criterion c]). Thus, naïve birds appeared key to populations’ transition to the improved (quicker) solution by overcoming experienced individuals’ tendency to stick with their practiced methods (Chimento et al., 2021).

Because transmission chains and the replacement method are usually not feasible with chimpanzees (discussed in detail later in the article), recent studies have employed “closed-group” or “open-diffusion” task designs (Whiten & Mesoudi, 2008). Typically, these tasks involve training a chimpanzee on a behavior that subsequently serves as a model to the rest of their group. Davis et al. (2016) tested whether groups of chimpanzees would relinquish a practiced, inefficient solution for a more optimal (quicker) one introduced by a trained demonstrator. As with Marshall-Pescini and Whiten (2008a), chimpanzees generally perseverated on their inefficient behaviors and only switched to the more efficient behavior when their practiced technique became almost impossible to perform (see also Harrison & Whiten, 2018; Hopper et al., 2011; Hrubesch et al., 2009; Manrique & Call, 2011; but see Jacobson & Hopper, 2019). This indicated a degree of conservatism in chimpanzees, similar to that observed in great tits

(Chimento et al., 2021), where known behaviors interfered with the adoption of an alternative, more efficient one that was shown to be within their ability to invent (Davis et al., 2016; not meeting Criterion d)). Further investigation indicated that behavioral flexibility was linked to the solution complexity and payoff incentives: Chimpanzees switched from a simple, known behavior to a newly observed and better-paying solution of equal difficulty, but they more rarely relinquished known behaviors when they were complex or were of similar difficulty but not higher paying (Davis et al., 2019). Abandoning an act that may have taken considerable effort or practice to learn may show reluctance to forgo well-rehearsed techniques or habits that were known to achieve a goal and may explain behavioral stasis once a certain level of complexity is reached.

Similar closed-group designs have been used to examine whether chimpanzees can socially learn more complex (and efficient) solutions from a conspecific demonstrator (Vale, Davis, et al., 2017). Chimpanzees acquired behaviors that surpassed what individuals invented in the absence of any social information (in comparable conditions). However, groups of naïve chimpanzees appeared to pool their skills to discover the same behaviors. One individual discovered part of the behavioral sequence of interest (unscrewing a stop valve to make a functional straw) before a second individual used their discarded tool to obtain a juice reward, a sequence that spread to others, albeit at a slower rate and attained by fewer individuals than occurred in the model seeded groups. These data therefore only provide suggestive evidence for cumulative advancements in this technological (tool deconstruction) task because the role of social learning was not clear-cut (Criterion b). The same population of chimpanzees was recently tested on a task that afforded participants to construct, rather than deconstruct, tools to gain a progressively valuable reward (Vale et al., 2021). The complexity of solutions observed in groups did not surpass the complexity of those discovered by chimpanzees tested individually, indicating a lack of CCE (not meeting Criterion d). The differences in findings across studies maybe be explained by the type of tool modifications involved (i.e., construction/deconstruction), a point we discuss in more detail later in the article.

Chimpanzee Invention

Whether the complex behaviors observed in wild populations are cumulative has also been tested by exposing naïve, captive populations to the ecological conditions thought to be necessary for the behavior to occur. The logic is that if animals discover the same behaviors as their wild counterparts, we can conclude that (a) action copying was not necessarily required for the inception of the behavior, and (b) it does not surpass an individual’s capacity to develop through personal exposure to the right conditions. This work, by Tennie and colleagues, has focused on several wild chimpanzee tool-use behaviors, including pestle pounding, algae scooping, and nut-cracking (Bandini & Tennie, 2017, 2019, 2020; Neadle et al., 2020). In all cases except nut-cracking, chimpanzees were able to reinvent the behavior under the conditions provided in captive settings, suggesting they are within an individual’s capability to invent (their “zone of latent solutions” [ZLS]; Tennie et al., 2009, 2016).

There are several challenges to the ZLS, however. It is difficult to be certain that these animals, some of whom were wild born,

were truly naïve to these behaviors—the researchers rely upon keeper and caretaker testimony to document the animals' experience (Bandini & Tennie, 2017). A further concern is the omission of complex components of these behaviors that are typically needed in the wild. For example, the processes of finding, selecting, and fashioning the correct tool for the task are not typically required in captive tasks, where the chimpanzees are instead provisioned with usable tools from the outset (Bandini & Tennie, 2017). Notably, the objective of the task was to re-create the *act*, as a test for the role of form-copying in the examples from wild chimpanzees, and did not claim to be re-creating the entire behavior. For example, in an algae-scooping study, chimpanzees were provisioned with a stick to fish a floating piece of bread out of water, whereas in the wild, chimpanzees must first identify an appropriate stick (smooth or hooked) of adequate length, detach it, and even modify it by the removal of smaller branches or fraying of the ends (Boesch et al., 2017). Thus, although these studies suggest that at least some components of these behaviors exist in a ZLS, we encourage future studies to examine whether whole behavioral sequences can be reinvented rather than being just part of the action.

Research on CCE in nonhuman animals both from the wild and captivity is suggestive; however, it is not *conclusive* evidence of CCE. At present, notwithstanding evidence in nonprimate species that we discuss further later in the article, one of the most convincing cases from wild data is chimpanzee nut-cracking. This is because it can take years to master (Inoue-Nakamura & Matsuzawa, 1997), is not easily reinvented by naïve individuals (Neadle et al., 2020), and involves social learning (Marshall-Pescini & Whiten, 2008b). However, chimpanzees have been cracking nuts for thousands of years (Mercader et al., 2007), which raises questions regarding whether improvement has been made to this behavior—over millennia. Nevertheless, the behavioral change that might have predated the available archaeological record is also unknown (Whiten, 2021). Researchers working with captive populations or performing field experiments have documented improvements in behavioral efficiency across transmission chains of multiple participants (Chimento et al., 2021; Claidière et al., 2014; Sasaki & Biro, 2017). Open-diffusion experiments have also begun to show promise as a way to assess CCE, revealing modest increases in behavioral complexity (Vale, Carr, et al., 2017; but see Vale et al., 2021), and have created the opportunity to isolate some of the sociocognitive factors that may play a role in species' capacity for CCE (Davis et al., 2016; Dean et al., 2012). Many of these studies have also highlighted some of the difficulties of studying CCE and the associated methodological limitations they can impose in nonhumans (a subject discussed later), including assessment of CCE in nonprimates.

Cultural Evolution and CCE in Animal Song

Aside from primates, there is growing evidence for cultural evolution and perhaps CCE, particularly in the vocal displays of other animals. Although cultural transmission of vocalizations has been reported in diverse species (reviewed in Garland & McGregor, 2020), here we focus on two pertinent cases of potential CCE, in humpback whales and zebra finches, that show large-scale cultural shifts over time or change across laboratory learning generations.

Among whales, the songs produced by humpback males (*Megaptera novaeangliae*) are one of the most complex. These songs are long and hierarchically structured vocalizations, and populations of whales develop their own variants, or “local dialects,” through social learning (Noad et al., 2000; see Barker et al. [2021] for a recent example in naked mole rats and Watson et al. [2015] for a case in chimpanzees). Although a variety of animals display local dialects, few studies have explored whether animal vocalizations change over time. An exception is the songs of humpback whales that have now been subject to decades of study. Detailed recordings in the South Pacific have now revealed that their dialects evolve and change in “waves”; song variants socially transmit (Criteria a and b) eastward through neighboring populations (Garland et al., 2011). The scale of this cultural evolution is also vast, occurring across the Pacific Ocean basin, with songs repeatedly changing every few years (Garland et al., 2011; Noad et al., 2000). There is some indication that song complexity also changes, increasing as the songs evolve (Criterion c) but also decreasing in cases where complete song “revolutions” (replacements) occur (Allen et al., 2018). Although we do not yet know the complexity of humpback whale song in the absence of social information (uncertainty of Criterion d), which can be difficult to test in such large mammals, the repeated cultural change that propagates through multiple populations every few years (Garland et al., 2011) shows striking parallels to human CCE.

Song development in zebra finches has been tracked using experimental methods similar to those used to study CCE in humans. Typically, young male zebra finches learn their song by copying adult males (Criterion b), developing wild-type, local variants, with some individual variability (indicative of Criterion a). When deprived of this experience, however, young males develop a distinguishable, relatively unstructured “isolate” variant, allowing song “recovery,” or development, to be traced. Fehér et al. (2009) paired juvenile finches with isolate “tutor” birds before placing learners in transmission chains (pupils became the tutors for the next generation, and so forth). Similar to whale songs, finches' songs changed over learning events, recovering from isolate versions; similarity to the wild variant increased in just a few generations (suggestive of Criterion c but unknown if wild-type song represents an improvement). Furthermore, songs of later generations differed from the isolate songs, which is indicative of CCE (Criterion d). These findings mirror results from transmission-chain studies with human spoken language, where learnability and structure improve with iterated learning events between individuals (Kirby et al., 2008).

As these two examples illustrate, animal songs can change over time through repeated learning events between individuals, constituting interesting examples of cultural evolution, if not cumulative culture. Indeed, these, along with the cases described in baboons (Claidière et al., 2014) and pigeons (Sasaki & Biro, 2017), meet most or all of our criteria for CCE.

Evaluation of the Methods and Advancements

Despite the significant advances made over the past 2 decades, limitations remain for comparative research in terms of what can or cannot be assessed with nonhuman animals and the implications for CCE research. Specifically, issues concerning sample sizes, species comparability of motor and cognitive abilities, and participant

demographics may require addressing for the field to continue to move forward. We next describe these concerns and provide some suggestions for their resolution.

Sample Sizes

Accessing sufficient sample sizes (comparable to human research) is difficult when studying many nonhuman animal species (Sjoberg, 2017). Research facilities, sanctuaries, and zoos often have limited physical spaces and/or facilities, and ethical guidelines, correctly, encourage reducing the number of tested nonhuman animals to the smallest possible number. This means the number of social groups and the size of social and asocial samples are limited to relatively small numbers, and participants often have been subject to similar studies before (meaning they are not experimentally naïve). In no small part because humans are detrimentally affecting nonhuman primate population numbers and behavioral diversity (Estrada et al., 2017; Köhl et al., 2019), there are similar sample-size issues in the wild, where accessing and/or accurately tracking animals (or species) can be logistically difficult. The power to statistically detect effects is therefore difficult—particularly when using multiple comparisons—and the generalizability of findings is weakened. Although concerns regarding replicability have led to many disciplines addressing issues of sample sizes (Loken & Gelman, 2017), tackling this in some comparative research is not easily solved, given that generational and/or multigroup studies demand relatively large sample sizes, and many species of interest are not available in such numbers.

A potential way of increasing overall sample sizes and the numbers of groups is to pool data from multiple study sites, as has been done elsewhere (Altschul et al., 2019; Hopper, 2017; MacLean et al., 2014; van Leeuwen et al., 2020; Weiss et al., 2007; Whiten et al., 1999). When taking this approach, researchers should account for variables that may vary across sites, including exposure to humans, participant ages, testing experience, enrichment exposure, and group demographics (Altschul et al., 2019; discussed further later in the article). An alternative option is to maximize individual-level data. This can be done using aggregated data over repeated trials (or “generations”) within individuals, which would, theoretically, significantly reduce the number of participants required (Caldwell et al., 2020; Claidière et al., 2018). Assessment of CCE here would involve exposing individuals to social information of varying success levels and documenting evidence of improved performance over trials. However, we also note that this approach, which may be better suited to certain animal species, requires careful study design, and researchers should consider task-exposure effects (Caldwell et al., 2020).

Motor and Cognitive Abilities

A key methodological concern for any comparative study is to develop tasks that capture appropriate contextual validity for the species being examined. Multiple factors need to be considered, including whether study species have appropriate motor and cognitive capacities concerning the administered tasks. Designing experimental paradigms, tasks, and apparatuses that allow direct comparisons across animal species means considering whether specific actions are more difficult for one species than for another.

Tool-use and puzzle-box tasks for CCE research have allowed researchers to make direct (Dean et al., 2012; Tennie et al., 2009) and indirect (Davis et al., 2016; McGuigan & Whiten, 2009; Reindl et al., 2016; Whiten, 2017b) inferences regarding the socio-cognitive mechanisms underpinning CCE in humans and chimpanzees. An important consideration, however, is whether the level of dexterity required for task success is more or less challenging for a given species. Motor diversity is a key predictor of innovative and individual problem-solving abilities in birds, nonhuman primates, and children (Diquelou et al., 2016; Griffin et al., 2014; Griffin & Guez, 2014; Keen, 2011), and thus species differences in this domain may limit any potential comparative conclusions. Tasks that require fine motor skills, for example, may be better suited to humans than to other animals or may require a substantial period of training for nonhuman animals to reach the required criteria (Davis et al., 2019; Vale, Davis, et al., 2017). If significant training is required, this may also weaken comparisons to human studies in which participants require far less training for similar tasks. Animals learning tasks can also be required to observe humans (i.e., a heterospecific) face to face, requiring copying mirror images, whereas children are often adjacent to (i.e., a conspecific) experimenters, meaning they can use motor imitation.

Relatedly, the type of actions we ask of animals may have important implications for the study of CCE. For instance, deconstructing tools may be more species appropriate and ecologically valid than constructing ones for tool-using species (Bania et al., 2009). This is because in the wild, animals' tools are typically made and modified using broadly destructive, rather than constructive, actions, such as detaching probe sticks or leaf tools and trimming them (e.g., chimpanzees [Boesch et al., 2017], bearded capuchin monkeys [Mannu & Ottoni, 2009], New Caledonian crows [Hunt & Gray, 2003]). At our study site, the National Center for Chimpanzee Care (NCCC), individuals also fashion tools by detaching materials with greater ease than those that require combinatory actions, suggesting that this is not simply an artifact of what is readily available in the wild. In the first tool-construction task conducted at this site, 14 of 50 chimpanzees fashioned elongated tools by inserting one tool component into another (Price et al., 2009). However, very few chimpanzees beyond these have since demonstrated such skills, despite testing nearly the entire colony on various construction tasks (Neldner, 2020; Vale et al., 2016; Vale et al., 2021). For example, only 3 of 20 naïve chimpanzees recently tested on tool construction learned how to combine tools, and they failed to use them as a functional tool to gain an out-of-reach reward (Vale et al., 2016). Learning to deconstruct object components to make a functional tool or for exchange for a higher-valued reward, in contrast, has been relatively prevalent in our colony (Neldner, 2020; Vale, Davis, et al., 2017). Creating tasks that are species appropriate is therefore essential to avoid concluding that species lack certain skills when the outcome may be an artifact of specific task conditions (de Waal, 2016; Leavens et al., 2019).

Breeding in captive chimpanzee populations has been banned in the United States (and several other countries) since 2007 (Knight, 2008), meaning populations in many locations are aging, and there are very few juveniles or young chimpanzees available for testing. When dealing with many aging captive nonhuman primate populations, we must consider the effects of their cognitive abilities, motivation, and participation in experiments that vary across the

life span because these will ultimately have consequences on the conclusions we draw. Whether animals attempt and persist at tasks, for example, can decline with age (Barbary macaques, *Macaca sylvanus*; Rathke & Fischer, 2020), whereas perseveration with known solutions or strategies can increase (rhesus macaques; Lai et al., 1995; e.g., on aging and cognitive decline in other species, see Chapagain et al. [2020] for dogs, Kapellusch et al. [2018] for rats, and Kwapis et al. [2020] for mice). Openness, linked with cognitive performance, also changes over the chimpanzee life span—with males in particular decreasing over adulthood (Rawlings et al., 2020). Candidate CCE behaviors such as nut-cracking are cognitively demanding and can take years to master, and if aging populations are showing cognitive decline, these factors will have significant implications for studies of animal learning. CCE requires behavioral change, individual or group-level behavioral flexibility, and the motivation to learn often-complex new skills, and this may lead researchers to underestimate species' CCE abilities.

Sampling Biases

A decade ago, psychologists acknowledged an overreliance on so-called Western, educated, industrialized, rich, and democratic (WEIRD) human samples, which often perform at the extreme ends of continuums of psychological studies (Henrich et al., 2010). The pace of human cross-cultural research has rapidly increased over recent years—including within the field of CCE. As a result, the field has made and continues to make significant conceptual, theoretical, and methodological improvements through the assessment of diverse populations (Broesch et al., 2020; Hruschka et al., 2018; Kline et al., 2018; Nielsen et al., 2017). A similar argument regarding nonhuman animal samples was raised at the same time: Individuals raised in captivity (i.e., barren, institutional, zoo, and other rare rearing environments [BIZARRE]) may not represent their wild counterparts (Leavens et al., 2010). Yet, comparative research has yet to fully address the issue of sampling biases (Webster & Rutz, 2020), where individual and group-level factors affect which species and participants engage in behavioral research. Despite extensive and valuable investment in studying wild populations, sampling biases have important implications for the generalizability of data and conclusions that can be drawn from CCE studies.

At the individual level, factors such as personality, dominance status, prior testing experience, social status, and rearing history are important causes of selection bias (Altschul et al., 2017; Brosnan et al., 2015; Herrelko et al., 2012; Hopper et al., 2014; Morton et al., 2013; Rawlings et al., 2020). Much of primate behavioral research is based on voluntary participation, for good reason, but this also means that individuals who enjoy testing and/or are high ranking enough are most likely to participate, and indeed, they may act as trained demonstrators—which affects subsequent learning of behaviors in groups (Kendal et al., 2015; Vale et al., 2021; Watson et al., 2017). At the group level, nonhuman animals raised in captive contexts may not be representative of the species at large. Frequent caregiver interaction and exposure to enrichment activities or behavioral testing may skew behavior and task performance, as does interaction with tasks through bars, making comparisons with wild or even other captive populations and children difficult (Haslam, 2013; Leavens et al., 2019). Conversely,

captive environments are comparatively impoverished—as a function of less stimulation, contextual diversity, and fewer group members—compared with natural conditions (Boesch, 2007). Further, in many research sites, nonhuman primate groups have been rearranged or moved locations, which can have a significant impact on social bonds and social-based research (Dufour et al., 2011; Schel et al., 2013), as can environmental uncertainty (Galef & Whiskin, 2004). Implementing steps to overcome selection bias is crucial for a fairer representation of the population intended to be examined (Morton et al., 2013; Webster & Rutz, 2020).

Here we reiterate the recent STRANGE framework proposed by Webster and Rutz (2020), which provides an assessment tool that researchers can use to identify if their sample is representative of the larger population of interest. Seven categories are identified, namely, the subject's social background, trappability and self-selection, rearing history, acclimation and habituation, natural changes in responsiveness, genetic makeup, and experience (i.e., STRANGE). These categories highlight, for example, that some individuals may be more motivated to participate than others (trappability and self-selection) and more or less likely to solve particular tasks depending on their previous experience and rearing conditions. Researchers interested in CCE may find this a useful framework to assess samples' representativeness and how it may be improved. For example, self-selection biases may be reduced by testing social groups, by testing for extended periods to overcome potential task monopolization, or by introducing multiple tasks or stimuli so that more than one subject can participate at any given time. Variation in subject rearing histories and experimental experience, if known, can also be controlled for either statistically or in the research design (Bandini, 2021; Neadle et al., 2020; Vale et al., 2021). Implementing comparable testing setups between species will also allow for fairer comparisons (McGuigan et al., 2017; Neldner, 2020).

The STRANGE framework is therefore a useful tool for researchers to present information about their study group, which allows fairer conclusions on the generalizability of the findings. We also fully acknowledge that it is not always possible to control the fact that a sample is STRANGE. Work on such samples has provided a wealth of key knowledge on the evolutionary basis of CCE, and with breeding bans across many institutions, nonhuman primate researchers are running out of opportunities to collect such data. We suggest in such cases that comparative researchers fully and openly acknowledge the sample biases. Doing so will avoid the extreme data collected from STRANGE samples to become interpreted as the default of the entire species.

Likewise, comparisons between the cultural learning strategies of human children and nonhuman animals have been a valuable line of research for establishing the ontogeny of CCE (Dean et al., 2012; 2014; Tennie et al., 2009; Vale, Flynn, et al., 2017). Yet, as with primates, while the field is beginning to assess diverse populations, the vast majority of experimental CCE research on children has involved WEIRD populations. This bias presents issues with the conclusions that can be drawn when comparing children's performance with that of other species, and researchers should be mindful of the human population in which they study. Tools such as STRANGE frameworks could usefully be applied to developmental research to improve assessment of the generalizability of findings, which may also have similar biases within populations. Children who have caregivers who actively consent to participate

in scientific studies and children who willingly participate in research, for example, can generate selection biases (Anderman et al., 1995). As with nonhuman animal studies, we encourage CCE researchers interested in development to evaluate, report, and improve the representativeness of their samples.

The Value of Observational and Experimental Approaches

Although much of our focus has been on experimental work, our intention is not to prioritize this method over observational approaches. Experiments are not feasible with certain species (e.g., large animals such as whales; Janson & Brosnan, 2013) and can lack external validity. Observational approaches, by contrast, afford documentation and evaluation of naturally occurring candidate CCE behaviors (Henrich, 2015; Noad et al., 2000; Reyes-García et al., 2016), which can be highly informative of species' natural behaviors as well as useful for planning experiments. The use of both approaches is required to make crucial and complementary contributions to the field of comparative CCE.

Bridging the gap between experimental laboratory work and observational research are field experiments, which have become an important tool for understanding how animal cultures emerge and spread within groups in natural settings. Field experiments involve using experiments in wild populations of animals, often to study naturally occurring behaviors (Aplin et al., 2015; Biro et al., 2003; Gruber et al., 2009; Sasaki & Biro, 2017; van de Waal et al., 2014). The core value of field experiments is thus that they provide experimental control while studying animals in their natural habitat. Indeed, arguably the strongest evidence for nonhuman CCE, based on our criteria, is the field experiment of navigational routes with homing pigeons (Sasaki & Biro, 2017). In many cases, they exceed the capacity of lab experiments because the question can be studied under a broader range of relevant contexts. Likewise, field experiments can also exceed the capacity of observational research due to the experimental control they provide. However, it is important to note that lab research typically allows more control and can usually offer additional manipulations. Field experiments can only be used to study what we know to examine, so we need observations to document behaviors occurring in their natural environment and how behaviors we observe in the lab manifest in the wild.

The continued use of field experiments, alongside other experimental and observational approaches, will be crucial to documenting the scope of CCE in the animal kingdom in ways not previously possible. The development of sophisticated technology and advanced methodological approaches is providing new methods to collect rich data on CCE in diverse species. Lightweight trackers and camera traps have allowed researchers to detail migration routes and improvements in spatial navigation in wild animals. Advanced statistical approaches, such as network-based diffusion analysis (NBDA), mean that scientists can document the advent and spread of innovations across dynamic social networks (Allen et al., 2013; Hobaiter et al., 2014; Migliano et al., 2020; Wild et al., 2019). Such tools will be valuable for understanding how the social environment affects CCE in natural conditions.

In humans, the vast majority of evidence for CCE in non-Western populations remains based on ethnographic data (Henrich, 2004; Reyes-García et al., 2016; Salali et al., 2016), which is

problematic from the perspective of understanding other species' CCE because these results are not comparable to those generated in lab and field experiments or observational research in nonhuman species. Fortunately, the recent growth of cross-cultural research means that mechanisms such as social learning and innovation are being studied experimentally in a broader range of populations (Berl & Hewlett, 2015; Clegg et al., 2017; Legare, 2017; Neldner et al., 2017; Nielsen et al., 2014; Rawlings et al., 2019). We encourage cross-cultural research to complement ethnographic studies with explicitly experimental CCE research in diverse populations, using ethical and equitable approaches (Broesch et al., 2020; Urassa et al., 2021). Additionally, we simultaneously encourage cross-cultural researchers to validate experimental tasks and paradigms to improve construct validity and thus the quality of explanations (Broesch et al., 2020; Hruschka et al., 2018; Kline et al., 2018; Lew-Levy et al., 2020). These steps will be essential for improving our understanding of how cultural diversity shapes the remarkable diversity of human CCE and how CCE evolved in humans and other species.

Directions for Future Research

We next discuss three key areas we believe are particularly pertinent to continuing to move the field of cumulative cultural evolution forward. We suggest that refining asocial control testing methods, addressing age differences in comparative studies, and continuing to broaden study species will be particularly beneficial for improving theory in future research.

Asocial Control Testing Methods

Crucial aspects of advancements in the field of CCE include the addition of asocial controls that examine an individual's invention abilities to provide a comparator for group-level achievements and transmission-chain designs that allow "generational" changes to occur across participants (Miton & Charbonneau, 2018; Reindl et al., 2020). For nonhuman animal research, however, these require individuals to be separated from their group, which may be undesirable for a social species and is not always possible for many species (particularly into individual isolation). Individuals may be reluctant to separate, or testing facilities may have regulations on whether and for how long individuals can be separated, and isolation can induce unnecessary stress upon participants (which can also reduce their willingness to participate or change their behavior). Transmission-chain studies, which involve dyadic testing, require careful consideration of differences in the dominance statuses between pairs of individuals. Moreover, researchers rarely consider wider contextual issues when comparing asocial to group performance. Individuals in asocial conditions may show increased vigilance compared with those in groups, and they lack opportunities for social facilitation that enhances activity based on the mere presence of others (Zajonc, 1965). Recent research shows that chimpanzees tested in social groups exhibited more diverse behavioral repertoires and had greater task success than participants tested in the absence of conspecifics (Vale et al., 2021). This suggests that social facilitatory effects and/or a larger pool of skills and motivations in groups can influence study results and that social settings should be considered by researchers as they design control conditions (see also Finestone et al., 2014).

These issues can prohibit researchers from using certain techniques or result in unbalanced study designs where, for example, few individuals form the asocial controls (or come from smaller groups) compared with much larger social groups. Although this is often necessary, it is problematic because we often do not know if individuals would reach the same solutions as groups would if given the same cumulative exposure time or if more control individuals were tested (see Table 1).

One potential solution is to test individuals in the presence of others (either in dyads or groups, although dyadic testing faces similar separation and dominance issues as transmission-chain studies). Similar to asocial controls, such naïve groups can provide baselines for groups that are seeded with animals trained on complex or efficient solutions, although this method does not work as a comparator for unseeded groups. Dyads and control groups may also benefit from social facilitation, as well as reduced vigilance, thereby ruling this out as a potential explanation for any enhanced performance in experimental groups. Alternatively, the role of social learning can be assessed, even when control individuals necessarily receive shorter task exposure than groups, by controlling for test times or the number of trials participants engage in. That is, if groups are tested for longer periods or receive more trials, their data can be capped so that they are equivalent to asocial control durations. A note of caution is required with this latter method because researchers will need to ensure they provide a reasonable amount of time for subjects to develop the skill or behavior of interest.

Age Differences in Comparative Studies

Studies directly comparing humans and chimpanzees have been highly informative for our understanding of what sociocognitive mechanisms may distinguish human culture, including CCE, from one of our closest extant species. However, to our knowledge, all such studies have involved comparisons between human children (typically young children) and adult chimpanzees (Dean et al., 2012; Haun et al., 2014; McGuigan et al., 2017; Tennie et al., 2009; Vale et al., 2021; Vale, Flynn, et al., 2017; van Leeuwen et al., 2014). There are good reasons for this; by middle childhood, children begin to outperform chimpanzees on a range of cognitive and sociocognitive tasks, and thus using young children allows us to not conflate species differences in CCE behaviors with interspecies cognitive differences (Herrmann et al., 2007; Nielsen, 2009; Wobber et al., 2014). Relatedly, the tasks typically used in comparative research are relatively simple ones, such as puzzle boxes, for which adults would perform at ceiling (if the outcome variables are success based).

Nonetheless, despite these rationales, comparing young children to adult chimpanzees is also problematic for multiple reasons. First, developmental experiences, such as rearing conditions and maternal stress or deprivation, shape innovation and social learning propensities in a range of species, meaning that comparing samples at different life-history stages is problematic for interpretation (Bard & Leavens, 2014; Mesoudi et al., 2016). Second, there are also within-species age differences in children's and chimpanzees' cultural learning strategies. In nonhuman primates, surveys suggest that adults are more innovative than nonadults (Reader & Laland, 2001). Observational studies have shown that infancy and juvenility may be a sensitive period for chimpanzees

to socially acquire complex cultural behaviors, such as nut-cracking (Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2017; Lonsdorf et al., 2004). Likewise, young children are particularly reliant on copying others, but they become more innovative and less reliant on social information as they age through childhood (Carr et al., 2015; Rawlings, 2018). If this is the case, we would expect juvenile humans to behave differently from adult nonhuman primates based on age alone, invalidating these purported species differences. Third, from middle age, chimpanzees show an age-related decline in performance on cognitive tasks (Hopkins et al., 2021), meaning that drawing meaningful conclusions from comparing young children to older chimpanzees on cognitive-based tasks is difficult. This is particularly relevant in studies that use captive chimpanzees because this population is heavily biased toward older individuals.

Given these challenges, it is important for researchers to include age-period-matched samples across species when possible or at least to discuss the potential confounds. Comparing young nonhuman primates with human children will allow for direct comparisons of how development shapes the ontogeny of CCE in both species. Given breeding bans, particularly in chimpanzees, this will be difficult in some locations (i.e., research sites in the United States), but in situations in which it is possible, such as in zoos and in the wild, we can use these data to help interpret non-age-matched studies. This is also another context in which initiatives such as the ManyPrimates project, in which researchers collaboratively pool individuals from multiple sites, would be particularly beneficial (Altschul et al., 2019). Finally, few studies have compared adult humans and chimpanzees. As noted, running such studies can be difficult if the unit of measurement is simply success in solving a given task, but tasks can be designed to capture cumulative improvement in other ways. Documenting time to success, propensity to engage in certain behaviors, and the maximum level of complexity or efficiency reached would allow for adult comparisons of both species.

Broadening Study Species

An issue within comparative psychology has been a focus on too few model species, and the study of CCE is no exception, with its heavy focus on primates, particularly chimpanzees. Although recent years have seen a widening range of species studied, there is still much to learn about CCE in the wider animal kingdom. Indeed, promising findings from species such as bighorn sheep (Jesmer et al., 2018), Savannah sparrows (Williams et al., 2013), humpback whales (Allen et al., 2013; Garland et al., 2011, 2017), zebra finches (Fehér et al., 2009), new Caledonian crows (Hunt & Gray, 2003), and bumblebees (Loukola et al., 2017) are indicative that diversifying species in CCE studies is important for a richer understanding of its extent beyond humans and its evolutionary origins. For example, bumblebees (*Bombus* spp.) developed more efficient ways of solving a ball-pulling task after receiving social information (Loukola et al., 2017), and the songs of a population of Savannah sparrows (*Passerculus sandwichiensis*) were found to vary over 3 decades in a manner that increased fitness (Williams et al., 2013).

Studying other species is critical to gain a richer understanding of nonhuman behavior; however, taxa such as birds or bumblebees also offer some methodological advantages over nonhuman primates.

Logistically, it may be easier to recruit larger sample sizes and/or implement generational studies in smaller-bodied and/or shorter-lived species. It may also be easier to make use of natural behaviors with certain species (e.g., songs or migration routes), which improves ecological validity. In addition, the greater variety of natural behaviors available across the entire animal kingdom increases the number of questions that can be answered relative to studying only primates. For instance, we can ask questions such as the following: Is CCE more common in material culture or communication? Is it more common in long-lived organisms in which individuals have extensive opportunities to learn from one another, or in shorter-lived organisms in which there may be particular advantages to learning from others? As we continue to diversify our study species, these questions can be addressed, and in turn, more questions will emerge.

Relatedly, nonhuman primate CCE research has largely focused on tool-use behaviors. As the increasing evidence of forms of CCE in domains outside of tool use—and with species that do not use tools frequently—shows, such a focus may be impeding theoretical progress. Although we acknowledge that studying, for example, social conventions and communication can be difficult, experimentally expanding the way in which we study CCE is key to advancing the field. Expanding longitudinal data collection (Jesmer et al., 2018; Schofield et al., 2018) to measure if and how CCE emerges in these domains is an important step to diversify our understanding of the contexts in which CCE occurs.

Perhaps most critically, throughout comparative psychology, there is a bias toward assuming that multistep and/or highly social behaviors, such as CCE, are complex and therefore require large brains, an assumption that has repeatedly been proven false (e.g., empathetic responding in rats [Ben-Ami Bartal et al., 2011], interspecific cooperation in moray eels and grouper [Bshary et al., 2006], and visual individual recognition in wasps [Tibbetts, 2002]). Knowing which species show aspects of CCE and how it may vary across organisms is required to both fully understand what behavioral mechanisms are essential and to better understand extant variability. For example, there are clear differences in what can be accomplished by humans with language and chimpanzees without, but language obscures other, less obvious factors; studying the variability in other species helps identify how these factors shape CCE as well.

Concluding Remarks

The cumulative nature of human culture is unquestionably distinct from all other species, yet the question of nonhuman animal CCE remains an open one. The marked increase in CCE research, both within the primates and more broadly across species, over the last 2 decades has significantly improved our understanding of its cognitive underpinnings, its ontogenetic and evolutionary origins, and the extent to which it exists outside of humans. Comparative research has been crucial to identifying cross-species similarities and differences in cultural behaviors and, ultimately, to identifying the key mechanisms underpinning the uniqueness of human cumulative cultural evolution. As the field has developed, however, researchers have used different criteria to determine CCE, which has led to studies that are not directly comparable. The field of primatology has critically improved our knowledge of CCE through the collection of data from multiple sites, both in captivity and in wild settings and longitudinally. Yet it also suffers from small

samples, making generalizability difficult, and primates are long-lived organisms for which generational studies are nearly impossible. We propose that a combination of stricter definitions, more robust methods, and a broader phylogenetic scope will allow us to more fully understand the evolution and development of CCE and, therefore, better understand what, if any, aspects of it are unique to humans and how our behavior fits into that of the rest of the animal kingdom.

References

- Acerbi, A., Kendal, J., & Tehrani, J. J. (2017). Cultural complexity and demography: The case of folktales. *Evolution and Human Behavior*, 38(4), 474–480. <https://doi.org/10.1016/j.evolhumbehav.2017.03.005>
- Allen, J., Garland, E. C., Dunlop, R. A., & Noad, M. J. (2018). Cultural revolutions reduce complexity in the songs of humpback whales. *Proceedings of the Royal Society B: Biological Sciences*, 285(1891), Article 20182088. <https://doi.org/10.1098/rspb.2018.2088>
- Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, 340(6131), 485–488. <https://doi.org/10.1126/science.1231976>
- Altschul, D. M., Beran, M. J., Bohn, M., Call, J., DeTroy, S., Duguid, S. J., Egelkamp, C. L., Fichtel, C., Fischer, J., Flessert, M., Hanus, D., Haun, D. B. M., Haux, L. M., Hernandez-Aguilar, R. A., Herrmann, E., Hopper, L. M., Joly, M., Kano, F., Keupp, S., . . . Watzek, J. (2019). Establishing an infrastructure for collaboration in primate cognition research. *PLoS ONE*, 14(10), Article e0223675. <https://doi.org/10.1371/journal.pone.0223675>
- Altschul, D. M., Wallace, E. K., Sonnweber, R., Tomonaga, M., & Weiss, A. (2017). Chimpanzee intellect: Personality, performance and motivation with touchscreen tasks. *Royal Society Open Science*, 4(5), Article 170169. <https://doi.org/10.1098/rsos.170169>
- Anderman, C., Cheadle, A., Curry, S., Diehr, P., Shultz, L., & Wagner, E. (1995). Selection bias related to parental consent in school-based survey research. *Evaluation Review*, 19(6), 663–674. <https://doi.org/10.1177/0193841X9501900604>
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518(7540), 538–541. <https://doi.org/10.1038/nature13998>
- Bandini, E. (2021). Implementing long-term baselines into primate tool-use studies. *American Journal of Primatology*, 83(1), Article e23224. <https://doi.org/10.1002/ajp.23224>
- Bandini, E., & Tennie, C. (2017). Spontaneous reoccurrence of “scooping”, a wild tool-use behaviour, in naïve chimpanzees. *PeerJ*, 5, Article e3814. <https://doi.org/10.7717/peerj.3814>
- Bandini, E., & Tennie, C. (2019). Individual acquisition of “stick pounding” behavior by naïve chimpanzees. *American Journal of Primatology*, 81(6), Article e22987. <https://doi.org/10.1002/ajp.22987>
- Bandini, E., & Tennie, C. (2020). Exploring the role of individual learning in animal tool-use. *PeerJ*, 8, Article e9877. <https://doi.org/10.7717/peerj.9877>
- Bania, A. E., Harris, S., Kinsley, H. R., & Boysen, S. T. (2009). Constructive and deconstructive tool modification by chimpanzees (*Pan troglodytes*). *Animal Cognition*, 12(1), 85–95. <https://doi.org/10.1007/s10071-008-0173-0>
- Bard, K. A., & Leavens, D. A. (2014). The importance of development for comparative primatology. *Annual Review of Anthropology*, 43(1), 183–200. <https://doi.org/10.1146/annurev-anthro-102313-030223>
- Barker, A. J., Vevirko, G., Bennett, N. C., Hart, D. W., Mograby, L., & Lewin, G. R. (2021). Cultural transmission of vocal dialect in the naked

- mole-rat. *Science*, 371(6528), 503–507. <https://doi.org/10.1126/science.abc6588>
- Beck, W. (1992). La preparación Aboriginál de las semillas de *Cycas* en Australia [Aboriginal preparation of *Cycas* seeds in Australia]. *Economic Botany*, 46(2), 133–147. <https://doi.org/10.1007/BF02930628>
- Ben-Ami Bartal, I., Decety, J., & Mason, P. (2011). Empathy and pro-social behavior in rats. *Science*, 334(6061), 1427–1430. <https://doi.org/10.1126/science.1210789>
- Berl, R. E. W., & Hewlett, B. S. (2015). Cultural variation in the use of overimitation by the Aka and Ngandu of the Congo Basin. *PLoS ONE*, 10(3), Article e0120180. <https://doi.org/10.1371/journal.pone.0120180>
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition*, 6(4), 213–223. <https://doi.org/10.1007/s10071-003-0183-x>
- Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology*, 12(2), 82–91. <https://doi.org/10.1002/evan.10106>
- Boesch, C. (2007). *What makes us human (Homo sapiens)? The challenge of cognitive cross-species comparison*. <https://doi.org/10.1037/0735-7036.121.3.227>
- Boesch, C., Bombjaková, D., Meier, A., & Mundry, R. (2019). Learning curves and teaching when acquiring nut-cracking in humans and chimpanzees. *Scientific Reports*, 9(1), Article e22613. <https://doi.org/10.1038/s41598-018-38392-8>
- Boesch, C., Kalan, A. K., Agbor, A., Arandjelovic, M., Dieguez, P., Lapeyre, V., & Köhl, H. S. (2017). Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea. *American Journal of Primatology*, 79(3), 1–7. <https://doi.org/10.1002/ajp.22613>
- Boesch, C., Kalan, A. K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, E. A., Barciela, A., Coupland, C., Egbe, V. E., Eno-Nku, M., Michael Fay, J., Fine, D., Adriana Hernandez-Aguilar, R., Hermans, V., Kadam, P., Kambi, M., Llana, M., Maretti, G., . . . Köhl, H. S. (2020). Chimpanzee ethnography reveals unexpected cultural diversity. *Nature Human Behaviour*, 4(9), 910–916. <https://doi.org/10.1038/s41562-020-0890-1>
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. University of Chicago Press.
- Boyd, R., & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. In W. G. Runciman, J. M. Smith, & R. I. M. Dunbar (Eds.), *Proceedings of the British Academy, Vol. 88: Evolution of social behaviour patterns in primates and man* (pp. 77–93). Oxford University Press.
- Boyd, R., Richerson, P. J., & Henrich, J. (2011). The cultural niche: Why social learning is essential for human adaptation. *Proceedings of the National Academy of Science of the United States of America*, 108 (Suppl. 2), 10918–10925. <https://doi.org/10.1073/pnas.1100290108>
- Boyd, R., Richerson, P. J., Henrich, J., & Lupp, J. (2013). The cultural evolution of technology: Facts and theories. In P. J. Richerson & M. H. Christiansen (Eds.), *Cultural evolution: Society, language, and religion* (Vol. 12, pp. 119–142). MIT Press.
- Broesch, T., Crittenden, A. N., Beheim, B. A., Blackwell, A. D., Bunce, J. A., Collier, H., Hagel, K., Kline, M., McElreath, R., Nelson, R. G., Pisor, A. C., Prall, S., Pretelli, I., Purzycki, B., Quinn, E. A., Ross, C., Scelza, B., Starkweather, K., Stieglitz, J., & Mulder, M. B. (2020). Navigating cross-cultural research: methodological and ethical considerations. *Proceedings of the Royal Society B: Biological Sciences*, 287(1935), Article 20201245. <https://doi.org/10.1098/rspb.2020.1245>
- Brosnan, S. F., Hopper, L. M., Richey, S., Freeman, H. D., Talbot, C. F., Gosling, S. D., Lambeth, S. P., & Schapiro, S. J. (2015). Personality influences responses to inequity and contrast in chimpanzees. *Animal Behaviour*, 101, 75–87. <https://doi.org/10.1016/j.anbehav.2014.12.019>
- Bshary, R., Hohner, A., Ait-el-Djoudi, K., & Fricke, H. (2006). Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. *PLoS Biology*, 4(12), Article e431. <https://doi.org/10.1371/journal.pbio.0040431>
- Byrne, R. W., & Byrne, J. M. E. (1993). Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): Variability and standardization. *American Journal of Primatology*, 31(4), 241–261. <https://doi.org/10.1002/ajp.1350310402>
- Caldwell, C. A. (2020). Using experimental research designs to explore the scope of cumulative culture in humans and other animals. *Topics in Cognitive Science*, 12(2), 673–689. <https://doi.org/10.1111/tops.12391>
- Caldwell, C. A., Atkinson, M., Blakey, K. H., Dunstone, J., Kean, D., Mackintosh, G., Renner, E., & Wilks, C. E. H. (2020). Experimental assessment of capacities for cumulative culture: Review and evaluation of methods. *WIREs Cognitive Science*, 11(1), Article e1516. <https://doi.org/10.1002/wcs.1516>
- Caldwell, C. A., Atkinson, M., & Renner, E. (2016). Experimental approaches to studying cumulative cultural evolution. *Current Directions in Psychological Science*, 25(3), 191–195. <https://doi.org/10.1177/0963721416641049>
- Caldwell, C. A., & Millen, A. E. (2008). Studying cumulative cultural evolution in the laboratory. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 363(1509), 3529–3539. <https://doi.org/10.1098/rstb.2008.0133>
- Caldwell, C. A., & Millen, A. E. (2009). Social learning mechanisms and cumulative cultural evolution. Is imitation necessary? *Psychological Science*, 20(12), 1478–1483. <https://doi.org/10.1111/j.1467-9280.2009.02469.x>
- Caldwell, C. A., Renner, E., & Atkinson, M. (2018). Human teaching and cumulative cultural evolution. *Review of Philosophy and Psychology*, 9(4), 751–770. <https://doi.org/10.1007/s13164-017-0346-3>
- Carr, K., Kendal, R. L., & Flynn, E. G. (2015). Imitate or innovate? Children's innovation is influenced by the efficacy of observed behaviour. *Cognition*, 142, 322–332. <https://doi.org/10.1016/j.cognition.2015.05.005>
- Chapagain, D., Wallis, L. J., Range, F., Affenzeller, N., Serra, J., & Virányi, Z. (2020). Behavioural and cognitive changes in aged pet dogs: No effects of an enriched diet and lifelong training. *PLoS ONE*, 15(9), Article e0238517. <https://doi.org/10.1371/journal.pone.0238517>
- Chimento, M., Alarcón-Nieto, G., & Aplin, L. M. (2021). Population turnover facilitates cultural selection for efficiency in birds. *Current Biology*, 9822(21), 430–439. <https://doi.org/10.1016/j.cub.2021.03.057>
- Claidière, N., Amedon, G. K., André, J.-B., Kirby, S., Smith, K., Sperber, D., & Fagot, J. (2018). Convergent transformation and selection in cultural evolution. *Evolution and Human Behavior*, 39(2), 191–202. <https://doi.org/10.1016/j.evolhumbehav.2017.12.007>
- Claidière, N., Smith, K., Kirby, S., & Fagot, J. (2014). Cultural evolution of systematically structured behaviour in a non-human primate. *Proceedings of the Royal Society B: Biological Sciences*. Advance online publication. <https://doi.org/10.1098/rspb.2014.1541>
- Clegg, J. M., Wen, N. J., & Legare, C. H. (2017). Is non-conformity WEIRD? Cultural variation in adults' beliefs about children's competency and conformity. *Journal of Experimental Psychology: General*, 146(3), 428–441. <https://doi.org/10.1037/xge0000275>
- Coelho, C. G., Falótico, T., Izar, P., Mannu, M., Resende, B. D., Siqueira, J. O., & Ottoni, E. B. (2015). Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.). *Animal Cognition*, 18(4), 911–919. <https://doi.org/10.1007/s10071-015-0861-5>
- Davis, S. J., Schapiro, S. J., Lambeth, S. P., Wood, L. A., & Whiten, A. (2019). Behavioral conservatism is linked to complexity of behavior in chimpanzees (*Pan troglodytes*): Implications for cognition and cumulative culture. *Journal of Comparative Psychology*, 133(1), 20–35. <https://doi.org/10.1037/com0000123>
- Davis, S. J., Vale, G. L., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2016). Foundations of cumulative culture in apes: Improved foraging efficiency through relinquishing and combining witnessed behaviours in

- chimpanzees (*Pan troglodytes*). *Scientific Reports*, 6, Article 35953. <https://doi.org/10.1038/srep35953>
- de Waal, F. B. M. (2016). *Are we smart enough to know how smart animals are?* (1st ed.). Norton.
- Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, 335(6072), 1114–1118. <https://doi.org/10.1126/science.1213969>
- Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2014). Human cumulative culture: A comparative perspective. *Biological Reviews of the Cambridge Philosophical Society*, 89(2), 284–301. <https://doi.org/10.1111/brv.12053>
- Dere, M., & Mesoudi, A. (2020). Cumulative cultural evolution within evolving population structures. *Trends in Cognitive Sciences*, 24(8), 654–667. <https://doi.org/10.1016/j.tics.2020.04.005>
- Diquelou, M. C., Griffin, A. S., & Sol, D. (2016). The role of motor diversity in foraging innovations: A cross-species comparison in urban birds. *Behavioral Ecology*, 27(2), 584–591. <https://doi.org/10.1093/beheco/arv190>
- Dufour, V., Sueur, C., Whiten, A., & Buchanan-Smith, H. M. (2011). The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *American Journal of Primatology*, 73(8), 802–811. <https://doi.org/10.1002/ajp.20943>
- Eshchar, Y., Izar, P., Visalberghi, E., Resende, B., & Frigaszy, D. (2016). When and where to practice: Social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Animal Cognition*, 19(3), 605–618. <https://doi.org/10.1007/s10071-016-0965-6>
- Estienne, V., Cohen, H., Wittig, R. M., & Boesch, C. (2019). Maternal influence on the development of nut-cracking skills in the chimpanzees of the Taï forest, Côte d'Ivoire (*Pan troglodytes verus*). *American Journal of Primatology*, 81(7), Article e23022. <https://doi.org/10.1002/ajp.23022>
- Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K. A.-I., Nijman, V., Heymann, E. W., Lambert, E., Rovero, F., Barelli, C., Setchell, J. M., Gillespie, T. R., Mittermeier, R. A., Verde Arregoitia, L., de Guinea, M., Gouveia, S., Dobrovolski, R., . . . Li, B. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, 3(1), e1600946. <https://doi.org/10.1126/sciadv.1600946>
- Fay, N., De Kleine, N., Walker, B., & Caldwell, C. A. (2019). Increasing population size can inhibit cumulative cultural evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 116(14), 6726–6731. <https://doi.org/10.1073/pnas.1811413116>
- Fehér, O., Wang, H., Saar, S., Mitra, P. P., & Tchernichovski, O. (2009). De novo establishment of wild-type song culture in the zebra finch. *Nature*, 459(7246), 564–568. <https://doi.org/10.1038/nature07994>
- Finestone, E., Bonnie, K. E., Hopper, L. M., Vreeman, V. M., Lonsdorf, E. V., & Ross, S. R. (2014). The interplay between individual, social, and environmental influences on chimpanzee food choices. *Behavioural Processes*, 105, 71–78. <https://doi.org/10.1016/j.beproc.2014.03.006>
- Fiore, A. M., Cronin, K. A., Ross, S. R., & Hopper, L. M. (2020). Food cleaning by Japanese macaques: Innate, innovative or cultural? *Folia Primatologica*, 91(4), 433–444. <https://doi.org/10.1159/000506127>
- Galef, B. G., Jr., & Whiskin, E. E. (2004). Effects of environmental stability and demonstrator age on social learning of food preferences by young Norway rats. *Animal Behaviour*, 68(4), 897–902. <https://doi.org/10.1016/j.anbehav.2003.10.029>
- Garland, E. C., Goldizen, A. W., Rekdahl, M. L., Constantine, R., Garrigue, C., Hauser, N. D., Poole, M. M., Robbins, J., & Noad, M. J. (2011). Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Current Biology*, 21(8), 687–691. <https://doi.org/10.1016/j.cub.2011.03.019>
- Garland, E. C., & McGregor, P. K. (2020). Cultural transmission, evolution, and revolution in vocal displays: Insights from bird and whale song. *Frontiers in Psychology*, 11, Article 544929. <https://doi.org/10.3389/fpsyg.2020.544929>
- Garland, E. C., Rendell, L., Lamoni, L., Poole, M. M., & Noad, M. J. (2017). Song hybridization events during revolutionary song change provide insights into cultural transmission in humpback whales. *Proceedings of the National Academy of Sciences of the United States of America*, 114(30), 7822–7829. <https://doi.org/10.1073/pnas.1621072114>
- Griffin, A. S., Diquelou, M. C., & Perea, M. (2014). Innovative problem solving in birds: A key role of motor diversity. *Animal Behaviour*, 92, 221–227. <https://doi.org/10.1016/j.anbehav.2014.04.009>
- Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common mechanisms. *Behavioural Processes*, 109, 121–134. <https://doi.org/10.1016/j.beproc.2014.08.027>
- Gruber, T., Luncz, L., Mörchen, J., Schuppli, C., Kendal, R. L., & Hockings, K. (2019). Cultural change in animals: A flexible behavioural adaptation to human disturbance. *Palgrave Communications*, 5(1), Article 64. <https://doi.org/10.1057/s41599-019-0271-4>
- Gruber, T., Muller, M. N., Strimling, P., Wrangham, R., & Zuberbühler, K. (2009). Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Current Biology*, 19(21), 1806–1810. <https://doi.org/10.1016/j.cub.2009.08.060>
- Gruber, T., Poisot, T., Zuberbühler, K., Hoppitt, W., & Hobaiter, C. (2015). The spread of a novel behavior in wild chimpanzees: New insights into the ape cultural mind. *Communicative & Integrative Biology*, 8(2), Article e1017164. <https://doi.org/10.1080/19420889.2015.1017164>
- Haidle, M. N., & Schladt, O. (2020). Where does cumulative culture begin? A plea for a sociologically informed perspective. *Biological Theory*, 15(3), 161–174. <https://doi.org/10.1007/s13752-020-00351-w>
- Harrison, R. A., & Whiten, A. (2018). Chimpanzees (*Pan troglodytes*) display limited behavioural flexibility when faced with a changing foraging task requiring tool use. *PeerJ*, 6, Article e4366. <https://doi.org/10.7717/peerj.4366>
- Haslam, M. (2013). “Captivity bias” in animal tool use and its implications for the evolution of hominin technology. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences*, 368(1630), Article 20120421. <https://doi.org/10.1098/rstb.2012.0421>
- Haun, D. B. M., Rekers, Y., & Tomasello, M. (2014). Children conform to the behavior of peers; other great apes stick with what they know. *Psychological Science*, 25(12), 2160–2167. <https://doi.org/10.1177/0956797614553235>
- Henrich, J. (2004). Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses: The Tasmanian case. *American Antiquity*, 69(2), 197–214. <https://doi.org/10.2307/4128416>
- Henrich, J. (2015). *The secret of our success: How culture is driving human evolution, domesticating our species, and making us smarter*. Princeton University Press. <https://doi.org/10.2307/j.ctvc77f0d>
- Henrich, J., & Henrich, N. (2010). The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proceedings of the Royal Society B: Biological Sciences*, 277(1701), 3715–3724. <https://doi.org/10.1098/rspb.2010.1191>
- Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences*, 33(2–3), 61–83. <https://doi.org/10.1017/S0140525X0999152X>
- Herrelko, E. S., Vick, S.-J. J., & Buchanan-Smith, H. M. (2012). Cognitive research in zoo-housed chimpanzees: Influence of personality and impact on welfare. *American Journal of Primatology*, 74(9), 828–840. <https://doi.org/10.1002/ajp.22036>
- Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, 317(5843), 1360–1366. <https://doi.org/10.1126/science.1146282>

- Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, 69(2), 207–231. <https://doi.org/10.1111/j.1469-185X.1994.tb01506.x>
- Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology*, 12(9), Article e1001960. <https://doi.org/10.1371/journal.pbio.1001960>
- Hohmann, G., & Fruth, B. (2003). Culture in bonobos? Between-species and within-species variation in behavior. *Current Anthropology*, 44(4), 563–571. <https://doi.org/10.1086/377649>
- Hopkins, W. D., Maren, M. C., Neal Webb, S. J., Schapiro, S. J., Raghanti, M. A., & Sherwood, C. C. (2021). Age-related changes in chimpanzee (*Pan troglodytes*) cognition: Cross-sectional and longitudinal analyses. *American Journal of Primatology*, 83(3), e23214. <https://doi.org/10.1002/ajp.23214>
- Hopper, L. M. (2017). Cognitive research in zoos. *Current Opinion in Behavioral Sciences*, 16, 100–110. <https://doi.org/10.1016/j.cobeha.2017.04.006>
- Hopper, L. M., Price, S. A., Freeman, H. D., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (2014). Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Animal Cognition*, 17(4), 835–847. <https://doi.org/10.1007/s10071-013-0715-y>
- Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour*, 81(6), 1195–1202. <https://doi.org/10.1016/j.anbehav.2011.03.002>
- Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, 8(3), 164–181. <https://doi.org/10.1007/s10071-004-0239-6>
- Hrubesch, C., Preuschoft, S., & van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Animal Cognition*, 12(2), 209–216. <https://doi.org/10.1007/s10071-008-0183-y>
- Hruschka, D. J., Munira, S., Jesmin, K., Hackman, J., & Tiokhin, L. (2018). Learning from failures of protocol in cross-cultural research. *Proceedings of the National Academy of Sciences of the United States of America*, 115(45), 11428–11434. <https://doi.org/10.1073/pnas.1721166115>
- Hunt, G. R., & Gray, R. D. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 270(1517), 867–874. <https://doi.org/10.1098/rspb.2002.2302>
- Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 111(2), 159–173. <https://doi.org/10.1037/0735-7036.111.2.159>
- Jacobson, S. L., & Hopper, L. M. (2019). Hardly habitual: Chimpanzees and gorillas show flexibility in their motor responses when presented with a causally-clear task. *PeerJ*, 7, Article e6195. <https://doi.org/10.7717/peerj.6195>
- Janson, C. H., & Brosnan, S. F. (2013). Experiments in primatology: From the lab to the field and back again. In E. Sterling, N. Bynum, and M. Blair (Eds.), *Primate ecology and conservation* (pp. 177–194). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199659449.003.0010>
- Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., Hurley, M. A., McWhirter, D. E., Miyasaki, H. M., Monteith, K. L., & Kauffman, M. J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science*, 361(6406), 1023–1025. <https://doi.org/10.1126/science.aat0985>
- Kapellusch, A. J., Lester, A. W., Schwartz, B. A., Smith, A. C., & Barnes, C. A. (2018). Analysis of learning deficits in aged rats on the W-track continuous spatial alternation task. *Behavioral Neuroscience*, 132(6), 512–519. <https://doi.org/10.1037/bne0000269>
- Keen, R. (2011). The development of problem solving in young children: A critical cognitive skill. *Annual Review of Psychology*, 62(1), 1–21. <https://doi.org/10.1146/annurev.psych.031809.130730>
- Kendal, R., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: Implications for cultural diversity. *Evolution and Human Behavior*, 36(1), 65–72. <https://doi.org/10.1016/j.evolhumbehav.2014.09.002>
- Kirby, S., Cornish, H., & Smith, K. (2008). Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. *Proceedings of the National Academy of Sciences of the United States of America*, 105(31), 10681–10686. <https://doi.org/10.1073/pnas.0707835105>
- Kline, M. A., Shamsudheen, R., & Broesch, T. (2018). Variation is the universal: making cultural evolution work in developmental psychology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1743), Article 20170059. <https://doi.org/10.1098/rstb.2017.0059>
- Knight, A. (2008). The beginning of the end for chimpanzee experiments? *Philosophy, Ethics, and Humanities in Medicine*, 3(1), Article 16. <https://doi.org/10.1186/1747-5341-3-16>
- Kühl, H. S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., Bocksberger, G., McElreath, M. B., Agbor, A., Angedakin, S., Ayimisin, E. A., Bailey, E., Barubiyo, D., Bessone, M., Brazzola, G., Chancellor, R., Cohen, H., Coupland, C., Danquah, E., . . . Kalan, A. K. (2019). Human impact erodes chimpanzee behavioral diversity. *Science*, 363(6434), 1453–1455. <https://doi.org/10.1126/science.aau4532>
- Kwapis, J. L., Alaghband, Y., Keiser, A. A., Dong, T. N., Michael, C. M., Rhee, D., Shu, G., Dang, R. T., Matheos, D. P., & Wood, M. A. (2020). Aging mice show impaired memory updating in the novel OUL updating paradigm. *Neuropsychopharmacology*, 45(2), 337–346. <https://doi.org/10.1038/s41386-019-0438-0>
- Lai, Z. C., Moss, M. B., Killiany, R. J., Rosene, D. L., & Herndon, J. G. (1995). Executive system dysfunction in the aged monkey: Spatial and object reversal learning. *Neurobiology of Aging*, 16(6), 947–954. [https://doi.org/10.1016/0197-4580\(95\)02014-4](https://doi.org/10.1016/0197-4580(95)02014-4)
- Laland, K. N., & Galef, B. G. (2009). *The question of animal culture*. Harvard University Press.
- Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, 21(10), 542–547. <https://doi.org/10.1016/j.tree.2006.06.005>
- Leavens, D. A., Bard, K. A., & Hopkins, W. D. (2010). BIZARRE chimpanzees do not represent “the chimpanzee.” *Behavioral and Brain Sciences*, 33(2–3), 100–101. <https://doi.org/10.1017/S0140525X10000166>
- Leavens, D. A., Bard, K. A., & Hopkins, W. D. (2019). The mismeasure of ape social cognition. *Animal Cognition*, 22, 487–504. <https://doi.org/10.1007/s10071-017-1119-1>
- Legare, C. H. (2017). Cumulative cultural learning: Development and diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 114(30), 7877–7883. <https://doi.org/10.1073/pnas.1620743114>
- Legare, C. H. (2019). The development of cumulative cultural learning. *Annual Review of Developmental Psychology*, 1(1), 119–147. <https://doi.org/10.1146/annurev-devpsych-121318-084848>
- Legare, C. H., & Nielsen, M. (2020). Ritual explained: Interdisciplinary answers to Tinbergen's four questions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1805), Article e31. <https://doi.org/10.1098/rstb.2019.0419>
- Lew-Levy, S., Milks, A., Lavi, N., Pope, S. M., & Friesem, D. E. (2020). Where innovations flourish: An ethnographic and archaeological overview of hunter-gatherer learning contexts. *Evolutionary Human Sciences*, 2, 1–61. <https://doi.org/10.1017/ehs.2020.35>

- Liebal, K., & Haun, D. B. M. (2012). The importance of comparative psychology for developmental science. *International Journal of Developmental Science*, 6(1–2), 21–23. <https://doi.org/10.3233/DEV-2012-11088>
- Loken, E., & Gelman, A. (2017). Measurement error and the replication crisis. *Science*, 355(6325), 584–585. <https://doi.org/10.1126/science.aal3618>
- Lonsdorf, E. V. (2017). Sex differences in nonhuman primate behavioral development. *Journal of Neuroscience Research*, 95(1–2), 213–221. <https://doi.org/10.1002/jnr.23862>
- Lonsdorf, E. V., Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, 428(6984), 715–716. <https://doi.org/10.1038/428715a>
- Loretto, M. C., Schuster, R., Federspiel, I. G., Heinrich, B., & Bugnyar, T. (2020). Contextual imitation in juvenile common ravens, *Corvus corax*. *Animal Behaviour*, 163, 127–134. <https://doi.org/10.1016/j.anbehav.2020.03.007>
- Loukola, O. J., Solvi, C., Coscos, L., & Chittka, L. (2017). Bumblebees show cognitive flexibility by improving on an observed complex behavior. *Science*, 355(6327), 833–836. <https://doi.org/10.1126/science.aag2360>
- Luncz, L. V., & Boesch, C. (2014). Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. *American Journal of Primatology*, 76(7), 649–657. <https://doi.org/10.1002/ajp.22259>
- Luncz, L. V., Sirianni, G., Mundry, R., & Boesch, C. (2018). Costly culture: Differences in nut-cracking efficiency between wild chimpanzee groups. *Animal Behaviour*, 137, 63–73. <https://doi.org/10.1016/j.anbehav.2017.12.017>
- Luther, D. A., & Derryberry, E. P. (2012). Birdsongs keep pace with city life: Changes in song over time in an urban songbird affects communication. *Animal Behaviour*, 83(4), 1059–1066. <https://doi.org/10.1016/j.anbehav.2012.01.034>
- MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., Aureli, F., Baker, J. M., Bania, A. E., Barnard, A. M., Boogert, N. J., Brannon, E. M., Bray, E. E., Bray, J., Brent, L. J. N., Burkart, J. M., Call, J., Cantlon, J. F., Cheke, L. G., . . . Zhao, Y. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences of the United States of America*, 111(20), E2140–E2148. <https://doi.org/10.1073/pnas.1323533111>
- Mannu, M., & Ottoni, E. B. (2009). The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the Caatinga: Tool making, associative use, and secondary tools. *American Journal of Primatology*, 71(3), 242–251. <https://doi.org/10.1002/ajp.20642>
- Manrique, H. M., & Call, J. (2011). Spontaneous use of tools as straws in great apes. *Animal Cognition*, 14(2), 213–226. <https://doi.org/10.1007/s10071-010-0355-4>
- Marshall-Pescini, S., & Whiten, A. (2008a). Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: An experimental approach. *Animal Cognition*, 11(3), 449–456. <https://doi.org/10.1007/s10071-007-0135-y>
- Marshall-Pescini, S., & Whiten, A. (2008b). Social learning of nut-cracking behavior in East African sanctuary-living chimpanzees (*Pan troglodytes schweinfurthii*). *Journal of Comparative Psychology*, 122(2), 186–194. <https://doi.org/10.1037/0735-7036.122.2.186>
- Matsuzawa, T. (1994). Field experiments on use of stone tools by chimpanzees in the wild. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 351–370). Harvard University Press.
- McGrew, W. C. (1992). *Chimpanzee material culture*. Cambridge University Press. <https://doi.org/10.1017/CBO9780511565519.005>
- McGuigan, N., Burdett, E., Burgess, V., Dean, L., Lucas, A., Vale, G. L., & Whiten, A. (2017). Innovation and social transmission in experimental micro-societies: Exploring the scope of cumulative culture in young children. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1735), Article 20160425. <https://doi.org/10.1098/rstb.2016.0425>
- McGuigan, N., & Whiten, A. (2009). Emulation and “overemulation” in the social learning of causally opaque versus causally transparent tool use by 23- and 30-month-olds. *Journal of Experimental Child Psychology*, 104(4), 367–381. <https://doi.org/10.1016/j.jecp.2009.07.001>
- Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., & Boesch, C. (2007). 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences*, 104(9), 3043–3048. <https://doi.org/10.1073/pnas.0607909104>
- Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution*, 31(3), 215–225. <https://doi.org/10.1016/j.tree.2015.12.012>
- Mesoudi, A., & Thornton, A. (2018). What is cumulative cultural evolution? *Proceedings of the Royal Society B: Biological Sciences*, 285(1880), Article 20180712. <https://doi.org/10.1098/rspb.2018.0712>
- Migliano, A. B., Battiston, F., Viguier, S., Page, A. E., Dyble, M., Schläepfer, R., Smith, D., Astete, L., Ngales, M., Gomez-Gardenes, J., Latora, V., & Vinicius, L. (2020). Hunter-gatherer multilevel sociality accelerates cumulative cultural evolution. *Science Advances*, 6(9), Article eaax5913. <https://doi.org/10.1126/sciadv.aax5913>
- Miton, H., & Charbonneau, M. (2018). Cumulative culture in the laboratory: Methodological and theoretical challenges. *Proceedings of the Royal Society B: Biological Sciences*, 285(1879). <https://doi.org/10.1098/rspb.2018.0677>
- Morgan, T. J. H., Uomini, N. T., Rendell, L. E., Chouinard-Thuly, L., Street, S. E., Lewis, H. M., Cross, C. P., Evans, C., Kearney, R., de la Torre, I., Whiten, A., & Laland, K. N. (2015). Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nature Communications*, 6, Article 6029. <https://doi.org/10.1038/ncomms7029>
- Morton, F. B., Lee, P. C., & Buchanan-Smith, H. M. (2013). Taking personality selection bias seriously in animal cognition research: A case study in capuchin monkeys (*Sapajus apella*). *Animal Cognition*, 16(4), 677–684. <https://doi.org/10.1007/s10071-013-0603-5>
- Musgrave, S., Lonsdorf, E., Morgan, D., Prestipino, M., Bernstein-Kurtycz, L., Mundry, R., & Sanz, C. (2020). Teaching varies with task complexity in wild chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, 117(2), 969–976. <https://doi.org/10.1073/pnas.1907476116>
- Muthukrishna, M., & Henrich, J. (2016). Innovation in the collective brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1690), Article 20150192. <https://doi.org/10.1098/rstb.2015.0192>
- Neadle, D., Bandini, E., & Tennie, C. (2020). Testing the individual and social learning abilities of task-naïve captive chimpanzees (*Pan troglodytes* sp.) in a nut-cracking task. *PeerJ*, 8(3), Article e8734. <https://doi.org/10.7717/peerj.8734>
- Neldner, K. (2020). *The development and evolution of tool innovation in human children (Homo sapiens) and chimpanzees (Pan troglodytes): A cross-cultural and comparative investigation* [Doctoral dissertation, University of Queensland]. <https://doi.org/10.14264/uql.2020.949>
- Neldner, K., Mushin, I., & Nielsen, M. (2017). Young children’s tool innovation across culture: Affordance visibility matters. *Cognition*, 168, 335–343. <https://doi.org/10.1016/j.cognition.2017.07.015>
- Nielsen, M. (2009). The imitative behaviour of children and chimpanzees: A window on the transmission of cultural traditions. *Revue de Primatologie*. Advance online publication. <https://doi.org/10.4000/primatologie.254>
- Nielsen, M., Haun, D., Kärtner, J., & Legare, C. H. (2017). The persistent sampling bias in developmental psychology: A call to action. *Journal of Experimental Child Psychology*, 162, 31–38. <https://doi.org/10.1016/j.jecp.2017.04.017>

- Nielsen, M., Tomaselli, K., Mushin, I., & Whiten, A. (2014). Exploring tool innovation: A comparison of Western and Bushman children. *Journal of Experimental Child Psychology*, 126, 384–394. <https://doi.org/10.1016/j.jecp.2014.05.008>
- Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M. N., & Jenner, K. C. S. (2000). Cultural revolution in whale songs. *Nature*, 408(6812), Article 537. <https://doi.org/10.1038/35046199>
- Norenzayan, A., & Gervais, W. M. (2011). The cultural evolution of religion. In E. Slingerland & M. Collard (Eds.), *Creating consilience: Integrating the sciences and the humanities* (pp. 243–265). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199794393.003.0014>
- Perry, S. (2011). Social traditions and social learning in capuchin monkeys (*Cebus*). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 366(1567), 988–996. <https://doi.org/10.1098/rstb.2010.0317>
- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., Manson, J. H., Panger, M., Pyle, K., & Rose, L. (2003). Social conventions in wild white-faced capuchin monkeys: Evidence for traditions in a neotropical primate. *Current Anthropology*, 44(2), 241–268. <https://doi.org/10.1086/345825>
- Perry, S. E., Barrett, B. J., & Godoy, I. (2017). Older, sociable capuchins (*Cebus capucinus*) invent more social behaviors, but younger monkeys innovate more in other contexts. *Proceedings of the National Academy of Sciences of the United States of America*, 114(30), 7806–7813. <https://doi.org/10.1073/pnas.1620739114>
- Price, E., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2009). A potent effect of observational learning on chimpanzee tool construction. *Proceedings of the Royal Society B: Biological Sciences*, 276(1671), 3377–3383. <https://doi.org/10.1098/rspb.2009.0640>
- Rathke, E.-M., & Fischer, J. (2020). Differential ageing trajectories in motivation, inhibitory control and cognitive flexibility in Barbary macaques (*Macaca sylvanus*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1811), Article 20190617. <https://doi.org/10.1098/rstb.2019.0617>
- Rawlings, B. (2018). *Establishing predictors of learning strategies; an investigation of the development of, and evolutionary foundations of, intrinsic and extrinsic factors influencing when we learn from others and from whom we learn* [Unpublished doctoral dissertation]. Durham University.
- Rawlings, B., Dutra, N., Turner, C., & Flynn, E. (2019). Overimitation across development: The influence of individual and contextual factors. In N. A. Jones, M. Platt, K. D. Mize, & J. Hardin (Eds.), *Conducting research in developmental psychology; a topical guide for research methods utilized across the lifespan* (pp. 26–39). Routledge. <https://doi.org/10.4324/9780429352065-2>
- Rawlings, B., Flynn, E., Freeman, H., Reamer, L., Schapiro, S. J., Lambeth, S., & Kendal, R. L. (2020). Sex differences in longitudinal personality stability in chimpanzees. *Evolutionary Human Sciences*, 2, Article e46. <https://doi.org/10.1017/ehs.2020.45>
- Rawlings, B., & Legare, C. H. (2021). Toddlers, tools, and tech: The cognitive ontogenesis of innovation. *Trends in Cognitive Sciences*, 25(1), 81–92. <https://doi.org/10.1016/j.tics.2020.10.006>
- Reader, S. M., & Laland, K. N. (2001). Primate innovation: Sex, age and social rank differences. *International Journal of Primatology*, 22(5), 787–805. <https://doi.org/10.1023/A:1012069500899>
- Reindl, E., Apperly, I. A., Beck, S. R., & Tennie, C. (2017). Young children copy cumulative technological design in the absence of action information. *Scientific Reports*, 7(1), Article 1788. <https://doi.org/10.1038/s41598-017-01715-2>
- Reindl, E., Beck, S. R., Apperly, I. A., & Tennie, C. (2016). Young children spontaneously invent wild great apes' tool-use behaviours. *Proceedings of the Royal Society B: Biological Sciences*, 283(1825), Article 20152402. <https://doi.org/10.1098/rspb.2015.2402>
- Reindl, E., Gwilliams, A. L., Dean, L. G., Kendal, R. L., & Tennie, C. (2020). Skills and motivations underlying children's cumulative cultural learning: Case not closed. *Palgrave Communications*, 6(1), 1–9. <https://doi.org/10.1057/s41599-020-0483-7>
- Reyes-García, V., Guèze, M., Díaz-Reviriego, I., Duda, R., Fernández-Llamazares, Á., Gallois, S., Napitupulu, L., Orta-Martínez, M., & Pyhälä, A. (2016). The adaptive nature of culture. A cross-cultural analysis of the returns of local environmental knowledge in three indigenous societies. *Current Anthropology*, 57(6), 761–784. <https://doi.org/10.1086/689307>
- Robbins, M. M., Ando, C., Fawcett, K. A., Grueter, C. C., Hedwig, D., Iwata, Y., Lodwick, J. L., Masi, S., Salmi, R., Stoinski, T. S., Todd, A., Vercellio, V., & Yamagiwa, J. (2016). Behavioral variation in gorillas: Evidence of potential cultural traits. *PLoS ONE*, 11(9), Article e0160483. <https://doi.org/10.1371/journal.pone.0160483>
- Salali, G. D., Chaudhary, N., Thompson, J., Grace, O. M., van der Burgt, X. M., Dyble, M., Page, A. E., Smith, D., Lewis, J., Mace, R., Vinicius, L., & Migliano, A. B. (2016). Knowledge-sharing networks in hunter-gatherers and the evolution of cumulative culture. *Current Biology*, 26(18), 2516–2521. <https://doi.org/10.1016/j.cub.2016.07.015>
- Saldana, C., Fagot, J., Kirby, S., Smith, K., & Claidière, N. (2019). High-fidelity copying is not necessarily the key to cumulative cultural evolution: A study in monkeys and children. *Proceedings of the Royal Society B: Biological Sciences*, 286(1904). <https://doi.org/10.1098/rspb.2019.0729>
- Sanz, C., Call, J., & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, 5(3), 293–296. <https://doi.org/10.1098/rsbl.2008.0786>
- Sasaki, T., & Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications*, 8(1), Article 15049. <https://doi.org/10.1038/ncomms15049>
- Schel, A. M., Rawlings, B., Claidière, N., Wilke, C., Wathan, J., Richardson, J., Pearson, S., Herrelko, E. S., Whiten, A., & Slocumbe, K. (2013). Network analysis of social changes in a captive chimpanzee community following the successful integration of two adult groups. *American Journal of Primatology*, 75(3), 254–266. <https://doi.org/10.1002/ajp.22101>
- Schofield, D. P., McGrew, W. C., Takahashi, A., & Hirata, S. (2018). Cumulative culture in nonhumans: Overlooked findings from Japanese monkeys? *Primates*, 59(2), 113–122. <https://doi.org/10.1007/s10329-017-0642-7>
- Sjoberg, E. A. (2017). Logical fallacies in animal model research. *Behavioral and Brain Functions*, 13(1), Article 3. <https://doi.org/10.1186/s12993-017-0121-8>
- Stewart, F. A., Pruett, J. D., & Hansell, M. H. (2007). Do chimpanzees build comfortable nests? *American Journal of Primatology*, 69(8), 930–939. <https://doi.org/10.1002/ajp.20432>
- Sugiyama, Y. (1997). Social tradition and the use of tool-composites by wild chimpanzees. *Evolutionary Anthropology*, 6(1), 23–27. [https://doi.org/10.1002/\(SICI\)1520-6505\(1997\)6:1<23::AID-EVAN7>3.0.CO;2-X](https://doi.org/10.1002/(SICI)1520-6505(1997)6:1<23::AID-EVAN7>3.0.CO;2-X)
- Sugiyama, Y., & Koman, J. (1979). Tool-using and -making behavior in wild chimpanzees at Bossou, Guinea. *Primates*, 20(4), 513–524. <https://doi.org/10.1007/BF02373433>
- Tehrani, J. J. (2013). The phylogeny of Little Red Riding Hood. *PLoS ONE*, 8(11), Article e78871. <https://doi.org/10.1371/journal.pone.0078871>
- Tennie, C., Braun, D. R., Premo, L. S., & McPherron, S. P. (2016). The island test for cumulative culture in the paleolithic. In M. N. Haide, N. J. Conard, & M. Bolus (Eds.), *The nature of culture* (pp. 121–133). Springer. https://doi.org/10.1007/978-94-017-7426-0_11
- Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences*, 364(1528), 2405–2415. <https://doi.org/10.1098/rstb.2009.0052>

- Tibbetts, E. A. (2002). Visual signals of individual identity in the wasp *Polistes fuscatus*. *Proceedings. Biological Sciences*, 269(1499), 1423–1428. <https://doi.org/10.1098/rspb.2002.2031>
- Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences*, 16(3), 495–511. <https://doi.org/10.1017/S0140525X0003123X>
- Urassa, M., Lawson, D. W., Wamoyi, J., Gurm, E., Gibson, M. A., Madhivanan, P., & Placek, C. (2021). Cross-cultural research must prioritize equitable collaboration *Nature Human Behaviour*. Advance online publication. <https://doi.org/10.1038/s41562-021-01076-x>
- Vale, G. L., Carr, K., Dean, L. G., & Kendal, R. L. (2017). The cultural capacity of human and nonhuman primates: Social learning, innovation, and cumulative cultural evolution. In J. H. Kaas (Ed.), *Evolution of nervous systems* (2nd ed., pp. 475–508). Elsevier. <https://doi.org/10.1016/B978-0-12-804042-3.00095-6>
- Vale, G. L., Davis, S. J., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2017). Acquisition of a socially learned tool use sequence in chimpanzees: Implications for cumulative culture. *Evolution and Human Behavior*, 38(5), 635–644. <https://doi.org/10.1016/j.evolhumbehav.2017.04.007>
- Vale, G. L., Flynn, E., Kendal, J., Rawlings, B., Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Kendal, R. (2017). Testing differential use of payoff-biased social learning strategies in children and chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 284(1868), Article 20171751. <https://doi.org/10.1098/rspb.2017.1751>
- Vale, G. L., Flynn, E. G., Pender, L., Price, E., Whiten, A., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (2016). Robust retention and transfer of tool construction techniques in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 130(1), 24–35. <https://doi.org/10.1037/a0040000>
- Vale, G. L., McGuigan, N., Burdett, E., Lambeth, S. P., Lucas, A., Rawlings, B., Schapiro, S. J., Watson, S. K., & Whiten, A. (2021). Why do chimpanzees have diverse behavioral repertoires yet lack more complex cultures? Invention and social information use in a cumulative task. *Evolution and Human Behavior*, 42(3), 247–258. <https://doi.org/10.1016/j.evolhumbehav.2020.11.003>
- van de Waal, E., Bshary, R., & Whiten, A. (2014). Wild vervet monkey infants acquire the food-processing variants of their mothers. *Animal Behaviour*, 90, 41–45. <https://doi.org/10.1016/j.anbehav.2014.01.015>
- van Leeuwen, E. J. C., Call, J., & Haun, D. B. (2014). Human children rely more on social information than chimpanzees do. *Biology Letters*, 10(11), Article 20140487. <https://doi.org/10.1098/rsbl.2014.0487>
- van Leeuwen, E. J. C., Staes, N., Verspeek, J., Hoppitt, W. J. E., & Stevens, J. M. G. (2020). Social culture in bonobos. In *Current Biology*, 30(6), R261–R262. <https://doi.org/10.1016/j.cub.2020.02.038>
- van Schaik, C. P. (2003). Local traditions in orangutans and chimpanzees: Social learning and social tolerance. In D. M. Frigaszy & S. E. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 297–328). Cambridge University Press. <https://doi.org/10.1017/CBO9780511584022.012>
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S., & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science*, 299(5603), 102–105. <https://doi.org/10.1126/science.1078004>
- Wasielowski, H. (2014). Imitation is necessary for cumulative cultural evolution in an unfamiliar, opaque task. *Human Nature*, 25(1), 161–179. <https://doi.org/10.1007/s12110-014-9192-5>
- Watson, S. K., Reamer, L. A., Mareno, M. C., Vale, G., Harrison, R. A., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2017). Socially transmitted diffusion of a novel behavior from subordinate chimpanzees. *American Journal of Primatology*, 79(6), Article e22642. <https://doi.org/10.1002/ajp.22642>
- Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., West, V., & Slocumbe, K. E. (2015). Vocal learning in the functionally referential food grunts of chimpanzees. *Current Biology*, 25(4), 495–499. <https://doi.org/10.1016/j.cub.2014.12.032>
- Webster, M. M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*, 582(7812), 337–340. <https://doi.org/10.1038/d41586-020-01751-5>
- Weiss, A., King, J. E., & Hopkins, W. D. (2007). A cross-setting study of chimpanzee (*Pan troglodytes*) personality structure and development: Zoological parks and Yerkes National Primate Research Center. *American Journal of Primatology*, 69(11), 1264–1277. <https://doi.org/10.1002/ajp.20428>
- Weston, S. J., & Jackson, J. J. (2018). The role of vigilance in the relationship between neuroticism and health: A registered report. *Journal of Research in Personality*, 73, 27–34. <https://doi.org/10.1016/j.jrp.2017.10.005>
- Whitehead, H., & Rendell, L. (Eds.). (2014). *The cultural lives of whales and dolphins*. University of Chicago Press. <https://doi.org/10.7208/chicago/9780226187426.001.0001>
- Whiten, A. (2017a). Culture extends the scope of evolutionary biology in the great apes. *Proceedings of the National Academy of Sciences of the United States of America*, 114(30), 7790–7797. <https://doi.org/10.1073/pnas.1620733114>
- Whiten, A. (2017b). Social learning and culture in child and chimpanzee. *Annual Review of Psychology*, 68(1), 129–154. <https://doi.org/10.1146/annurev-psych-010416-044108>
- Whiten, A. (2019). Cultural evolution in animals. *Annual Review of Ecology, Evolution, and Systematics*, 50(1), 27–48. <https://doi.org/10.1146/annurev-ecolsys-110218-025040>
- Whiten, A. (2021). The burgeoning reach of animal culture. *Science*, 372(6537), Article eabe6514. <https://doi.org/10.1126/science.abe6514>
- Whiten, A., Cusance, D. M., Gomez, J. C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110(1), 3–14. <https://doi.org/10.1037/0735-7036.110.1.3>
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, 138(11–12), 1481–1516. <https://doi.org/10.1163/156853901317367717>
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399(6737), 682–685. <https://doi.org/10.1038/21415>
- Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 364(1528), 2417–2428. <https://doi.org/10.1098/rstb.2009.0069>
- Whiten, A., & Mesoudi, A. (2008). Establishing an experimental science of culture: Animal social diffusion experiments. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences*, 363(1509), 3477–3488. <https://doi.org/10.1098/rstb.2008.0134>
- Wild, S., Allen, S. J., Krützen, M., King, S. L., Gerber, L., & Hoppitt, W. J. E. (2019). Multi-network-based diffusion analysis reveals vertical cultural transmission of sponge tool use within dolphin matriline. *Biology Letters*, 15(7), Article 20190227. <https://doi.org/10.1098/rsbl.2019.0227>
- Wilks, C. E. H., Rafetseder, E., Renner, E., Atkinson, M., & Caldwell, C. A. (2021). Cognitive prerequisites for cumulative culture are context-dependent: Children's potential for ratcheting depends on cue longevity. *Journal of Experimental Child Psychology*, 204, Article 105031. <https://doi.org/10.1016/j.jecp.2020.105031>
- Williams, H., Levin, I. I., Norris, D. R., Newman, A. E. M., & Wheelwright, N. T. (2013). Three decades of cultural evolution in

- Savannah sparrow songs. *Animal Behaviour*, 85(1), 213–223. <https://doi.org/10.1016/j.anbehav.2012.10.028>
- Wilson, W. M., & Dufour, D. L. (2002). Why “bitter” cassava? Productivity of “bitter” and “sweet” cassava in a Tukanoan Indian settlement in the northwest Amazon 1. *Economic Botany*, 56(1), 49–57. [https://doi.org/10.1663/0013-0001\(2002\)056\[0049:WBCPOB\]2.0.CO;2](https://doi.org/10.1663/0013-0001(2002)056[0049:WBCPOB]2.0.CO;2)
- Winters, J. (2019). Escaping optimization traps: The role of cultural adaptation and cultural exaptation in facilitating open-ended cumulative dynamics. *Palgrave Communications*, 5(1), Article 149. <https://doi.org/10.1057/s41599-019-0361-3>
- Wobber, V., Herrmann, E., Hare, B., Wrangham, R., & Tomasello, M. (2014). Differences in the early cognitive development of children and great apes. *Developmental Psychobiology*, 56(3), 547–573. <https://doi.org/10.1002/dev.21125>
- Yamamoto, S., Humle, T., & Tanaka, M. (2013). Basis for cumulative cultural evolution in chimpanzees: Social learning of a more efficient tool-use technique. *PLoS ONE*, 8(1), e55768. <https://doi.org/10.1371/journal.pone.0055768>
- Zajonc, R. B. (1965). Social facilitation. *Science* 149(3681), 269–274. <https://doi.org/10.1126/science.149.3681.269>
- Zwirner, E., & Thornton, A. (2015). Cognitive requirements of cumulative culture: Teaching is useful but not essential. *Scientific Reports*, 5, Article 16781. <https://doi.org/10.1038/srep16781>

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