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A Comparative Approach to the Study of Cumulative Cultural Evolution: Where Are We Now, and Where Do We Go?

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Evidence for cumulative cultural evolution (CCE) in nonhumans remains rare. Here, we suggest that this results partly from methodological challenges involved in comparative CCE. We discuss two core challenges researchers in the field face: our samples and our protocols. In particular, we encourage more studies that examine diverse species, adopt naturalistic and fair measures, and consider the life stages of participants. Research of this kind is required to fully understand the uniqueness of human CCE.

Keywords: cumulative cultural evolution, comparative cognition, nonhuman primates, social learning, methodology

This special issue provides a timely evaluation of the field of comparative cognition's future by encouraging researchers to reflect on questions and challenges warranting our attention. Here, we discuss a topic of significant interest for comparative scientists—that of cumulative cultural evolution (CCE) and the fundamental question of the uniqueness of human culture ("So Much," 2005; Whiten, 2021). Humans stand alone in the complexity and diversity of their culture, and it is widely held that our capacity for CCE—cycles of innovation and social learning allowing adaptive and cumulative improvements to skills, knowledge, and technology over historical time—is key to this success. Decades of research demonstrate that many animals, including invertebrates, invent new behaviors that are disseminated socially, which in some cases culminate in cultural traditions (Whiten, 2021). However, whether animals display CCE remains largely unknown. We argue that we must turn to the field of comparative cognition to ask whether more basic forms of cultural improvement occur across taxa, placing humans within the context of other animals. This includes investigating the scope and underlying cognitive architecture of nonhuman and human CCE, as well as factors influencing its expression. Through the lens of CCE we also stress limitations of the comparative approach, including the samples we test, our tasks, and procedures. We finish by outlining future directions for research in the field of comparative CCE.

Animal Studies of CCE: Where Are We Now?

The study of CCE now spans both human biological and social sciences, and this breadth recently encouraged Mesoudi and Thornton (2018) to introduce core criteria to help define it, incorporating central tenets of repeated episodes of invention and social learning that generate trait improvement. Although there are countless empirical and

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ethnographic examples of human CCE (Muthukrishna & Henrich, 2016), a recent comprehensive review documented just 26 nonhuman studies, spanning 13 species, empirically examining CCE directly or indirectly (Rawlings et al., 2021). Of these, fewer still met most or all the core criteria for CCE. Nevertheless, cultural refinements were broad in scope and species, including animal song (zebra finches: Fehér et al., 2009; humpback whales: Zandberg et al., 2021) migration pathways (bighorn sheep: Jesmer et al., 2018; pigeons: Sasaki & Biro, 2017), task-learnability (baboons: Claidière et al., 2014), and tool complexity (chimpanzees: Boesch et al., 2020; Vale et al., 2017).

Compelling cases of CCE in other species, which are likely to increase (Thornton & Mesoudi, 2023), challenge the view of CCE as a hallmark of human evolution. However, the dearth of overall studies and species studied highlights the need to devote greater research effort investment to understand the phylogenetic trajectory of CCE. The observed diversity in behavioral domains and taxa indicates that, in some cases, different (social) learning mechanisms and processes of cultural change may underpin these CCE or CCE-like behavioral outcomes (e.g., arising through emulation or imitation: Caldwell & Millen, 2009; Whiten et al., 2005; information pooling or collective intelligence: Sasaki & Biro, 2017; Vale et al., 2017; vocal imitation: Abramson et al., 2018; stimulus enhancement and observational learning: van der Post et al., 2016). The diversity also suggests convergent evolution, drawing attention to similar socioecological conditions (environment and selective pressures), may result in the independent evolution of cultural improvements over time rather than because of a shared ancestral trait (see Smith et al., 2018). Current considerations include an animal's innovative proclivities and their drivers (incentives/motivation to innovate), animal network structures that facilitate or impede their transmission (Thornton & Mesoudi, 2023; van Leeuwen & Goldsborough, 2023), and shifting from binary thinking about presence/absence to capturing the granularity of cultural variation and processes (Koops et al., 2023; Subiaul, 2023). We hope that these developments encourage future comparative scientists to expand the phylogenetic map of CCE and our understanding of its evolutionary drivers.

Where Should We Go Next and How Do We Get There? Challenges and Solutions in Comparative Studies of CCE

To continue to move forward, it is important to reflect on, and learn from, the pitfalls of past research. Like many areas of comparative cognition, limitations remain in what we can or cannot assess with nonhumans, with consequences for research on CCE (Rawlings et al., 2021). To provide future avenues to help guide the next generation of animal cultural studies, we next outline some of these challenges, including the samples tested and the tasks we present them.

Study Samples

For many species, accessing representative samples in sufficient numbers is highly challenging in both captive-focused and field-based settings. Institutions with managed populations are often limited in space, animals, staff, and the amount and type of research they support. Research in the wild is time, resource, and financially expensive, and population declines because of anthropogenic interference presents similar restrictions. These issues disproportionally impact candidate species for CCE who display rich cultural repertoires, such as nonhuman apes and cetaceans (van Leeuwen et al., 2020; van Schaik, 2003; Whiten et al., 1999). For studies of CCE, which focus on group-level processes, this can reduce statistical power and the broader application of findings.

Limited access to animals or difficulties running multigenerational studies may necessitate repeated testing of the same samples or testing individuals over multiple trials (Caldwell et al., 2020). Although important information is extracted in these cases, this approach introduces several confounds (Wood et al., 2023). Exemplars of such confounds occurring in captivity are the effects that housing institution (Forss et al., 2020), early life experiences (Salvanes et al., 2013), and the participant's research background (Vale et al., 2020) have on behavioral phenotypes, including skill competency and learning. Intraspecific variation also stems from familiarity levels that animals have with humans and task stimuli. Human-oriented animals can be more exploratory, more motivated, and less neophobic than less human-oriented ones (Damerius et al.,

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2017). Familiarity with resources and experimental stimuli also impact behavioral complexity of wild animals (e.g., bonnet macaques: Dhananjaya et al., 2022; Mangalam & Singh, 2013; although see Johnson-Ulrich et al., 2021). Intraspecific and population variation in neophobia, motivation, and novel behaviors and their complexity have clear consequences on comparative work on CCE that tests whether group-level traditions surpass in complexity and efficiency behaviors independently invented.

An obvious solution is to increase the number of animals we test (Brosnan et al., 2013; Smith et al., 2018). Big science initiatives, including the Many projects (e.g., ManyPrimates, ManyDogs, ManyBirds), are examples of cross-institutional collaborations to increase animal samples and improve the generalizability of findings (Altschul et al., 2019; Espinosa et al., 2021). There is also growing consensus for researchers to report animals' developmental backgrounds, which aids interpretation of species versus population-specific outcomes (Webster & Rutz, 2020). Finally, a key strength of comparative cognition is the use of complimentary observational and experimental approaches to study animals. CCE studies in particular showcase the power of these approaches, with each providing unique insights as well as challenges (Gilby & Machanda, 2022). Captive studies, for instance, afford greater experimental control by excluding potential confounds, allowing researchers to more confidently establish the presence of, and mechanisms driving, phenomena. However, they typically reduce ecological validity and involve contrived tasks. Conversely, observations of wild populations enable researchers to document behaviors in ecologies in which they evolve (Mertz et al., 2019) but offer little control over variables. Combining these approaches helps diversify the populations tested and strengthen inferences of the cultural transmission through direct experimental evidence of the mechanisms that can underpin putative cultural cases in the wild. Likewise, an integrated approach of field and captive-focused researchers working collaboratively improves our understanding of animal cognition and behavior across these types of contexts (Koops et al., 2023).

Study Protocols

Similarly, creating tasks that are closely matched or identical across species is challenging. Using the same or similar paradigms ensures that observed species differences or similarities represent true variation and are not artifacts of different methodologies. To our knowledge, however, just five comparative projects have used the same task to examine CCE in multiple species—and all involve human children and chimpanzees (Davis et al., 2016, 2022; Dean et al., 2012; McGuigan et al., 2017; Tennie et al., 2009; Vale et al., 2020). In this way, comparative CCE research falls behind many other areas of comparative cognition. We do recognize that designing tasks that capture constructs of interest in diverse species is difficult—particularly in CCE research, which requires measuring improvement over time as well as social, and often asocial, conditions. However, we argue that a major impediment to theoretical advancement in comparative CCE is a lack of more truly comparative tasks.

A related issue is whether comparative tasks are species appropriate or "fair" (Brosnan et al., 2013). The foundations of comparative CCE work are built on protocols comparing performance on tool-based tasks and artificial puzzleboxes, designed for species phylogenetically similar to humans (Davis et al., 2016, 2022; Dean et al., 2012; McGuigan et al., 2017; Tennie et al., 2009; Vale et al., 2020). These, and broader studies on cultural processes, have provided rich knowledge on species' differences and similarities in the mechanisms underpinning human and nonhuman primate CCE (Wood et al., 2023). Many of these projects have carefully considered the study species by designing tasks that mimic challenges experienced in the wild. However, researchers have argued that the tasks broadly used in comparative cognition can also be contrived and human-centric, and their lack of construct and external validity means they favor humans (Leavens et al., 2010, 2017; Rawlings et al., 2021). Others stress that paradigms that work well with one species can be inappropriate for, or interpreted differently by, others (Smith et al., 2018). It is unsurprising that the strongest evidence of CCE in nonhuman animals comes from studies using naturalistic tasks capturing the challenges the study species face in the wild (e.g., migration routes, extractive foraging, navigation). We encourage comparative researchers to continue to carefully design tasks and procedures to be "species fair" (Brosnan et al., 2013), inspired as much as possible by behaviors observed in the wild. We also encourage open-ended analogues or tasks that allow for an accumulation of solutions and problem generation, rather than reducing rich behaviors to simple component actions (Charbonneau et al., 2023; Koops et al., 2023; Whiten, 2022).

A more difficult challenge to overcome is comparing different species at similar life stages. Almost all comparative CCE studies involve comparing children to nonhuman primates (Rawlings et al., 2021)—though this problem is not restricted to CCE (Leavens et al., 2023). This approach

is used because children are argued to be less "enculturated" than adults, it avoids ceiling effects of human performance, and it reveals important developmental milestones in children. However, it has significant implications for how we interpret species differences in performance. As Leveans et al. (2023) pointed out, comparing human children to adult nonhuman primates makes it impossible to rule out ontogenetic explanations for any similarities or differences observed, over phylogenetic ones.

Concluding Remarks and Future Directions

We face many issues when studying comparative cognition. Here we focused on CCE and the challenges confronting us to determine the phylogenetic map of CCE and its evolutionary drivers. We argue that the key challenges facing comparative CCE research are the lack of diversity of taxa currently studied, limitations on the number of individuals one can study, the need for longitudinal studies, and the difficulty of designing experiments that are fair and naturalistic, while still being applicable across species. This area of research is ripe for exploration, especially given the increasingly sophisticated technology becoming more readily available to researchers. These include eye-trackers, camera traps, and animal trackers, which offer new avenues to explore CCE in diverse species and contexts and have already advanced our understanding of physical and social environmental impacts on CCE. Ultimately, as with wider comparative cognition research, there is a delicate balance between the capacity to make direct comparisons and the need for species-specific protocols. How quickly we reach this balance has important implications for the conclusions we draw regarding the uniqueness of human CCE, and whether, and to what extent, other species have evolved similar adaptations.

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