

Levelling the playing field in studying cumulative cultural evolution: conceptual and methodological advances in nonhuman animal research

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Abstract

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: cognition; comparative psychology; cumulative cultural evolution; innovation; nonhuman animals; culture; social learning.

1 Over recent decades, the topic of cumulative cultural evolution (CCE) – in which cycles of
2 innovation and social learning lead to adaptive modifications accumulating over historical
3 time - has become a focal topic in biological and social sciences (Caldwell & Millen, 2008;
4 Dean et al., 2014; Legare, 2017; Mesoudi & Thornton, 2018; Tennie et al., 2009). CCE is key
5 to the sophisticated technologies, customs and knowledge which pervade our lives, and is the
6 reason humans have such developments as complex social institutions, rituals, biomedicine,
7 agriculture, and literature (Boyd & Richerson, 1985; Henrich, 2015; Legare & Nielsen, 2020;
8 Muthukrishna & Henrich, 2016). Computers, for example, are not the invention of any one
9 individual, but are the product of centuries of cumulative cultural improvement; they have
10 evolved from steam-based analytical engines in the early 1800s, to Alan Turing’s seminal
11 machine capable of algorithmic logic, to large, single-circuit digital desktops computers, all
12 of which are products of building upon others’ output (with hundreds of iterations in
13 between), paving the way for the lightweight and computationally powerful laptops we use
14 today. Likewise, over generations, horticultural societies have developed sophisticated
15 processing techniques to process otherwise toxic foods, such as cycads and cassava to
16 provide new sources of food (Beck, 1992; Henrich & Henrich, 2010; Wilson & Dufour,
17 2002). Researchers have extensively examined what underpins CCE, its evolutionary origins
18 and whether it exists outside of humans, driven by the aim of understanding the success of
19 our species (reviewed in Caldwell et al., 2020; Dean et al., 2014; Tennie et al., 2009; Vale,
20 Carr, et al., 2017).

21

22 CCE has impacted all human cultures across a diverse set of domains, including knowledge
23 of foraging subsistence-oriented societies (Reyes-García et al., 2016; Salali et al., 2016), tool
24 complexity in Tasmania (Henrich, 2004), hunting techniques of the Central Inuit in the
25 Canadian Arctic (Boyd et al., 2013), structure and transmissibility of language (Kirby et al.,
26 2008) and folktales (Acerbi et al., 2017; Tehrani, 2013) as well as religious practices
27 (Norenzayan & Gervais, 2011). Key to CCE is the social dissemination of improved skills,
28 knowledge, behaviors and artifacts within groups that lead to adaptive changes. Many
29 nonhuman animal species are capable of social learning (learning by directly observing other
30 organisms or the byproducts of their actions, Heyes, 1994) and some even show cultural
31 traditions – group typical behavior that is socially transmitted (Laland & Janik, 2006).
32 Population-specific foraging, tool use, social and communicative behaviors across taxa such
33 as apes, monkeys, birds, and cetaceans are a result of the social transmission of these
34 behaviors within groups (Allen et al., 2013; Aplin et al., 2015; Gruber et al., 2015; van
35 Schaik, 2003a; Whitehead & Rendell, 2014; Whiten, 2019; Whiten et al., 1999). Yet,
36 concrete evidence for cultural change in a way that *cumulatively improves* existing skillsets
37 over time outside of humans remains elusive (Caldwell, 2020; Mesoudi & Thornton, 2018).
38 In particular, it may be challenging to show adaptive change over historical time in non-
39 human species, much less in experimental contexts, because their cultural traditions either
40 lack artifacts (i.e., are behavioral) or show less apparent change. However, while no other
41 species have anything close to our sophisticated technologies, symbolic languages and
42 institutions, as we present here, more basic forms of cultural improvement may be present
43 across a range of taxa (Wilks et al., 2021). Understanding these will help us understand the
44 evolutionary history of humans’ impressive capacity for cumulative culture.

45

46 Indeed, conclusions about the uniqueness of cumulative culture in humans may be precluded
47 by a lack of consistency in both the definitions and criteria used to determine CCE and the
48 methodology used to examine it across different animal species. Concerns regarding how
49 improvement is defined, whether it is measured the same way across studies, and whether
50 some criteria are empirically testable are of increasing interest to many researchers (Caldwell

51 et al., 2020; Mesoudi & Thornton, 2018; Miton & Charbonneau, 2018; Reindl et al., 2020;
52 Schofield et al., 2018). After all, inconsistent use of definitions means studies are not
53 comparable, making it difficult to assess how CCE may differ across contexts, much less
54 across different species. The latter of these is essential to understand the evolutionary history
55 of CCE and how it came to be such a dominant force in humans.

56

57 The primary goal of this paper is to provide a critical assessment of conceptual and
58 methodological advances within the field of CCE with respect to non-human animals. We
59 begin with a review of how definitions to assess CCE have evolved, particularly concerning
60 current debates surrounding scientific parsimony. After considering how these debates and
61 developments have impacted our ability to attribute CCE to nonhuman animals, we make
62 specific recommendations about which criteria should be used. We then use our
63 recommended criteria to assess the existing evidence from both wild and captive studies of
64 nonhuman animals, before discussing what research is needed going forward to advance the
65 field. Throughout the manuscript, we focus largely on nonhuman primates as, based on their
66 phylogenetic and cultural proximity to humans, they have been the focus of the majority of
67 nonhuman animal CCE research - particularly chimpanzees (Whiten, 2019). We also argue
68 that the field must continue to expand beyond primates however, and thus, where relevant,
69 we include literature from non-primates.

70

71 *The evolution of definitions and assessment of cumulative cultural evolution*

72

73 Early characterizations of cultural improvement were relatively broad, focusing on the
74 ‘ratchet effect’ - a process whereby the complexity of cultural traits (such as skills,
75 knowledge, technology, and customs that are transmitted socially within communities) are
76 improved through generations of innovations and their subsequent social transmission
77 (Tomasello et al., 1993). By this definition, cycles of modifications to, and ensuing social
78 dissemination of, cultural traits allow the ratcheting of knowledge with little/no ‘backward
79 slippage’ (loss of knowledge or reversion to previous, less efficient behaviour). These cycles
80 were suggested to culminate in products that no single individual could invent from scratch
81 within their lifetime (Boyd & Richerson, 1996; Dean et al., 2012, 2014). Attribution of
82 human uniqueness of CCE was based on the assumption that only humans possess the
83 required capacity for high fidelity social learning to faithfully maintain improvements over
84 time and prevent backward slippage. This view continues to be contentious, however, as (i)
85 similarly high-fidelity social learning may also be present in some nonhuman animals
86 (Boesch et al., 2020; Horner & Whiten, 2004; Loretto et al., 2020; Musgrave et al., 2020;
87 Whiten et al., 1996, 2009) and (ii) experimental research with humans has shown that
88 cumulative technological improvement can occur without high fidelity social learning
89 (Caldwell & Millen, 2009; Zwirner & Thornton, 2015, although see Wasielewski, 2014).

90

91 A large body of subsequent research has since highlighted theoretical and experimental
92 challenges to these early definitions (Caldwell et al., 2020; Dean et al., 2014; Haidle &
93 Schlaudt, 2020; Mesoudi & Thornton, 2018; Miton & Charbonneau, 2018; Reindl et al.,
94 2020; Schofield et al., 2018). For instance, while almost all researchers agree that CCE
95 requires cultural traits to show improvement over time by a process of building upon
96 previous generations (Caldwell, 2020; Davis et al., 2016; Dean et al., 2014; Legare, 2017;
97 Mesoudi & Thornton, 2018; Sasaki & Biro, 2017; Tennie et al., 2009; Weston & Jackson,
98 2018; Whiten, 2017a), improvement is not always defined or measured consistently. From an
99 evolutionary perspective, improvement should represent adaptive modifications over
100 historical time (Boyd et al., 2011; Derex & Mesoudi, 2020; Fay et al., 2019; Henrich, 2004,

101 2015; Winters, 2019), yet experiments only measure short term improvement rather than long
102 term adaptive changes. There is thus a disconnect between what, globally, we aim to know
103 about cumulative improvement, and what we can measure in laboratory settings.

104
105 Experimentally, improvement is typically described as an increase in complexity or
106 efficiency of a behavior (Dean et al., 2014), but these constructs themselves are
107 inconsistently measured (Schofield et al., 2018). Complexity, for example, can refer to the
108 number of behavioral steps or techno-units required to achieve a goal (Boesch et al., 2019;
109 Davis et al., 2019), differences in the hierarchical structure of behaviors (Boesch et al., 2019;
110 Byrne & Byrne, 1993) or overall level of difficulty (Caldwell et al., 2017). Efficiency can be
111 measured in terms of speed, learnability, a reduction of behavioral steps, calorie intake,
112 convenience, or security (Davis et al., 2016; Schofield et al., 2018; Stewart et al., 2007;
113 Yamamoto et al., 2013). Given that studies differ substantially in how they measure these
114 constructs, we suggest clearly stating units of measurements will provide clarity, help to
115 refine cross-study evaluations and will allow a clearer assessment of the impact of
116 improvement on other outcomes such as adaptive value, payoffs, or productivity (Schofield et
117 al., 2018).

118
119 A broader conceptual issue is that definitions of CCE may refer to both cultural processes
120 (cumulative improvement) or cultural products (behavioral outputs) (Reindl et al., 2020).
121 Process-based definitions, as defined by Reindl and colleagues, require improvements in
122 complexity or efficiency over generations of social transmissions but are not concerned with
123 the actual quantity of complexity or efficiency of the *final* product (McGuigan et al., 2017;
124 Mesoudi & Thornton, 2018). Product-based definitions, conversely, define the improved
125 complexity/efficiency as that which goes beyond what a naïve individual could invent within
126 their lifetime (Boyd & Richerson, 1996; Reindl et al., 2017, 2020; Tennie et al., 2016).
127 Researchers generally elect for either process or product-based definitions and this has
128 significant consequences for the underlying cognitive mechanisms involved (Rawlings &
129 Legare, 2021), the extent to which CCE is uniquely human or not, and even whether different
130 cohorts of the same species share CCE (e.g., children, adults, or both: Reindl et al., 2020).
131 Using different criteria also moves the goalposts concerning what is classified as CCE and
132 hinders our capacity to make fair cross-species comparisons, and thus to fully understand the
133 evolutionary origins of CCE. These issues also present important philosophical questions
134 regarding comparisons of CCE behavior between humans and nonhuman animals. To what
135 degree should researchers define phenomena such as CCE based on their experimental
136 tractability (i.e., process-based criteria)? Should we limit definitions to what is testable?
137 Study designs hinge on such questions; without tethering our definitions to empiricism, we
138 cannot scientifically evaluate them. Yet, capturing a phenomenon based on what is possible
139 to empirically examine risks overlooking very important aspects of the behavior (i.e.,
140 product-based criteria).

141
142 Further, the use of the criterion that CCE leads to traits (such as adaptive behaviours, skills or
143 artifacts) beyond which an individual can invent within their lifetime is increasingly being
144 questioned because it is impossible to experimentally examine in long lived species such as
145 humans and apes (Caldwell et al., 2016; Mesoudi & Thornton, 2018; Miton & Charbonneau,
146 2018; Schofield et al., 2018). This criterion emphasizes the power of collective knowledge
147 and provides a broader framework for CCE (in addition to measures of improvements in
148 complexity and efficiency). Experiments typically reduce generations or lifetimes to a matter
149 of minutes or hours, and thus cannot adequately or ethically assess whether a solitary

150 individual can invent a product of CCE in their lifetime (Mesoudi & Thornton, 2018; Miton
151 & Charbonneau, 2018).

152

153 In an attempt to overcome some of the definitional discrepancies outlined above, Mesoudi
154 and Thornton (2018) recently described both core and extended criteria for attributing CCE to
155 a population (which can be applied to assess CCE for any behavior found in a given
156 population, of any animal species). The core criteria, representing the minimum requirements
157 for a population to display CCE, include (i) a change in behavior (or product of behavior,
158 such as an artifact), typically due to asocial learning, followed by (ii) the transfer via social
159 learning of that novel or modified behavior to other individuals or groups, where (iii) the
160 learned behavior causes a performance improvement, which is a proxy of genetic and/or
161 cultural fitness, with (iv) the previous three steps repeated in a manner that generates
162 sequential improvement over time. According to this account, criteria i and ii equate to
163 cultural change (i.e., the transmission of innovations), the addition of criterion iii would be
164 evidence of cultural evolution (where the innovation causes improvement), and to distinguish
165 cultural evolution from cumulative cultural evolution, criteria iv is required (where this
166 improvement repeats over time). The extended criteria, which may or may not be present and
167 may be scaffolded by different socio-cognitive mechanisms than the core criteria, include i)
168 multiple functionally dependent cultural traits (for example, when new innovations are
169 contingent upon previous ones), ii) diversification into multiple lineages (such as different
170 types of projectile tools for hunting), iii) recombination across lineages (combining cultural
171 traits to develop new ones), and iv) cultural exaptation (i.e., a change in a cultural trait's
172 function), and v) cultural niche construction (i.e., where cultural traits impact the selective
173 environments of other biological or cultural traits). Criterion such as these provide a valuable
174 metric in which to classify candidate behaviours as evidence of CCE or not.

175

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

193

194 We propose that an extended criterion should include that these steps are repeated over
195 generations (which is core criterion iv from Mesoudi and Thornton, 2018), because for some
196 animal species, including nonhuman primates, assessing generational improvements is highly
197 difficult (Caldwell et al., 2020). In captivity, generational transmission chain experiments
198 (where information is passed along chains of individuals and improvement is measured) are
199 logistically problematic, requiring access to sufficient sample sizes and facilities that permit

200 this type of testing (issues discussed in detail later). Obtaining generational data from wild
201 populations requires longitudinal observations, which is equally, or more, difficult. Thus,
202 while we agree that evidence of invention and social spread leading to improvement (criteria
203 i-iii) being repeated over time would be optimal, it is not always feasible to measure.
204 Therefore, while we find the use of criterion extremely valuable for classifying behaviours as
205 evidence of CCE, we suggest that a more inclusive definition, applicable to diverse taxa may
206 also help further our understanding of the evolution of CCE. Using these criteria, we now
207 present and assess evidence of CCE in non-human primates and, where applicable, other
208 species, based on studies of wild and captive populations (Table 1).

209

210 *Cumulative culture in non-human animals: Evidence from wild and captive populations*

211

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

218

219 *CCE in non-human primates: Evidence from the wild*

220

221 Reports of group-level traditions in wild nonhuman primate populations, similar to human
222 culture, are now well-documented (see Boesch et al., 2019; McGrew, 1992; Whiten et al.,
223 1999 for chimpanzees [*Pan troglodytes*]; Hohmann & Fruth, 2003 for bonobos [*pan*
224 *paniscus*]; Perry, 2011 for capuchins [*genus Cebus*]; Robbins et al., 2016 for gorillas [*Gorilla*
225 *gorilla*]; van Schaik, 2003 for orangutans [*Pongo*]). Some of these traditions, such as
226 chimpanzee nut-cracking, vary in their complexity across populations, leading some to
227 suggest they have undergone successive refinements and that they, therefore, represent
228 examples of CCE (Boesch, 2003).

229

230 Perhaps the most famous traditions include chimpanzees' community-specific styles of
231 constructing and using tools during extractive foraging that are not easily attributed to
232 ecological or genetic dissimilarities. This strengthens the conclusion that these inventions
233 (criterion (i)) spread by social learning (criterion (ii)). Taking nut-cracking as one example,
234 chimpanzees in Bossou, Guinea, and Taï Forest, Côte d'Ivoire (Whiten et al., 2001) display
235 sophisticated procedures of using several tools to open the hard-shelled nuts found in their
236 habitats (see also Coelho et al., 2015 and Eshchar et al., 2016 for similar cases of nut-
237 cracking in capuchin monkeys). These two populations use wooden and stone hammers in
238 conjunction with an anvil, and more rarely, with a third component of a stone to stabilize the
239 anvil (Boesch et al., 2019; Luncz & Boesch, 2014; Matsuzawa, 1994; Sugiyama, 1997;
240 Sugiyama & Koman, 1979). Researchers have suggested that composite (two or more tools
241 used together to achieve a goal, here hammers and anvils) and compound tool use (combining
242 elements to make a single unit, here the wedge added to the anvil) represent elaborations of
243 the simpler percussive act of hitting (soft) shells with one's arm, or a single tool, perhaps
244 indicative of some form of CCE (Boesch, 2003). Neighboring groups' specificity in their
245 material selections also have consequences for the efficiency of these cultural traits, as
246 measured by foraging speed and the number of actions required to crack open nuts (Luncz et

247 al., 2018). However, while community differences in complexity and efficiency may indicate
248 trait modification, there is a lack of evidence of directionality to confirm that simple trait
249 variants preceded more sophisticated ones. Without such evidence, it is difficult to assert that
250 the behavior has undergone beneficial modifications (uncertainty of criterion (iii)).

251

252 A further concern here is whether the learned behaviors are beyond what may be invented by
253 a solitary chimpanzee in comparable conditions (criterion (iv)). This has also proven difficult
254 to test experimentally. Chimpanzees in the wild begin to successfully crack nuts by
255 approximately 3.5 years of age (Inoue-Nakamura & Matsuzawa, 1997) and master the
256 behavior when they are 5-6 years old (Estienne et al., 2019). Moreover, there appears to be a
257 sensitive period of between 3.5 and 10 years of age during which they can develop the skill
258 (Biro et al., 2003; Inoue-Nakamura & Matsuzawa, 1997; Matsuzawa, 1994). Both the
259 extended learning period and the limited age during which learning appears to occur make it
260 difficult to study in laboratory settings. A recent study found no evidence that 13 naive
261 captive chimpanzees, aged 10-52, would spontaneously crack nuts with tools after 92 hours
262 of practice (Neadle et al., 2020), which may suggest it is not easily invented. However, the
263 authors also reported no evidence that chimpanzees could socially learn this behavior,
264 perhaps suggesting that the chimpanzees either received too little exposure or were past the
265 sensitive period (Neadle et al., 2020). Indeed, in a group of 2–6-year-old chimpanzees,
266 individuals 3 years and over learned to crack open nuts on a stone anvil after observing con-
267 and hetero-specific demonstrations within days (Marshall-Pescini & Whiten, 2008a). This
268 contrasted an age-matched control group that showed no such learning until they received
269 social demonstrations (Marshall-Pescini & Whiten, 2008a), highlighting the importance of
270 social learning in the development of nut-cracking technologies during early chimpanzee
271 ontogeny.

272

273 Another case for CCE in chimpanzees has been made for their termite fishing behaviors. In a
274 large-scale study, Boesch et al. (2020) collated data from multiple chimpanzee communities,
275 documenting a detailed analysis of the technical elements they use to access termites.
276 Overall, there was impressive diversity in the techniques employed, with 38 different
277 elements involved, 30 of which could not easily be explained by community ecological
278 conditions. Some newly observed community-specific elements (*circumstantial* evidence of
279 inventions, criterion (i)), such as orientation, for instance by leaning on their elbow or lying
280 on their side, were suggested to have spread by social learning (criterion (ii)). Groups further
281 differed in the specific combinations of elements they used, some of which include tool
282 modifications (e.g., making of brush-tipped probes) that can lead to improvements in
283 behavioral efficiency (Sanz et al., 2009). Such community-specificity in the complexity of
284 the behavioral sequences used to extract termites, as with the nut-cracking example, resemble
285 cumulative additions to behaviors (see Boesch et al., 2020; Dean et al., 2014). Without
286 observation of its inception and development over time, however, we cannot be sure that
287 these behaviors evolved in complexity or efficiency (Boesch et al., 2020; although see Sanz
288 et al., 2009; criterion (iii)), nor that they exceed individuals' ability to invent (criterion (iv)).
289 Though individual discovery of the exact community-specific styles of termite fishing
290 (involving numerous behavioral elements) seems improbable, we cannot rule this out with
291 current data.

292

293 To circumvent speculation over the developmental course of recently observed traits,
294 researchers have examined long-term datasets spanning multiple generations (thus meeting
295 our extended criteria). Schofield et al. (2018) reviewed over 60 years of observations of
296 Japanese macaques' (*Macaca fuscata*) food-washing behaviors. This dataset included the first
297 instance of sweet potato washing followed by wheat washing (criterion (i)), allowing
298 researchers to track the spread (criterion (ii)) and progressive enhancements to these
299 behaviors since their inception (criterion (iii)). Various modifications were observed which
300 may represent cumulative increases in complexity and efficiency (Schofield et al., 2018).
301 Similar longitudinal observations have been conducted with white-faced capuchins (Perry,
302 2011; Perry et al., 2003, 2017), tracing the development and diffusion of a number of social
303 conventions, but there is question over whether they have improved over time, and their
304 reinvention suggests they do not surpass what individuals can invent for themselves (Dean et
305 al., 2014). Tracing innovations and behavioral change across generations is extremely time-
306 intensive, but promises to shed light on the cumulative cultural abilities of other species.
307 Although there remains a question over the role that social learning (criterion (ii)) plays in the
308 transmission of behaviors such as these, as it is not directly observed (Caldwell et al., 2020;
309 Fiore et al., 2020), we hope that continued observations of wild communities' inventions and
310 their spread will shed more light on whether CCE is shared with other animals.

311

312 *CCE in non-human primates: Experimental evidence*

313

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

330

331 The next study of CCE in nonhumans was by Dean and colleagues (2012), who took a
332 comparative approach on a larger scale, comparing the performance of group-housed
333 chimpanzees and capuchins to nursery aged children. Experiments that make such cross-
334 species comparisons are particularly important as they can identify trait similarities and
335 differences across species and shed light on their evolutionary histories (Liebal & Haun,
336 2012). All three species were posed an extractive foraging task similar to Marshall-Pescini
337 and Whiten (2008), but with three sequential and increasingly difficult steps that revealed
338 progressively valuable rewards (Dean et al., 2012). Whereas chimpanzees and capuchins had
339 difficulty in reaching complex task solutions, either by individually discovering them or by

340 learning socially from a proficient conspecific, many of the children quickly solved the task.
341 Children also displayed several socio-cognitive processes related to their task success that
342 were largely absent in the other primates, including sharing rewards (altruistic resource
343 donation) and knowledge (via teaching), as well as copying the actions of group members in
344 their group (imitation). High-fidelity social learning mechanisms, including imitation and
345 teaching, support the transmission of particularly complex knowledge or cultural traits, for
346 which other mechanisms, such as trying to recreate products through backward engineering
347 (emulation), may be insufficient (Caldwell et al., 2017; Morgan et al., 2015) and are thus
348 important contributors to the level of complexity a species can reach. This suite of
349 psychological processes were hence suggested to be key in supporting children's ability to
350 transition to more sophisticated and rewarding techniques, enabling them to outperform the
351 non-human participants (Legare, 2019).

352

353 A limitation of this study was the absence of an asocial control to ensure that individuals
354 could not independently solve the task (criterion (iv)). To address this, a new population of
355 children were tested on the same task previously presented to groups, to see if they could
356 solve the puzzlebox through personal exploration (Reindl et al., 2020). Notably, 9 out of 35
357 children discovered all three task levels without social demonstrations. Children in this study
358 failed to meet the authors' product-orientated definition of cumulative cultural evolution,
359 which requires the behavioral products of group tested participants to exceed those of
360 individuals (Reindl et al., 2020; criterion (iv)). Instead, the authors proposed that Dean et al.
361 (2012) had shown elementary cumulative cultural learning that was process orientated,
362 involving change through invention and social learning but without requiring the end result
363 (task level) to surpass what individuals could invent.

364

365 *Transmission chains, replacement methods and open diffusions*

366

367 Subsequent studies have experimentally examined CCE in other animals, including birds
368 (Sasaki & Biro, 2017) and baboons (Claidière et al., 2014), using transmission chains to
369 closed group open diffusion type tasks (described below) to reveal evidence for cultural
370 improvement. Transmission chain designs involve one participant, or 'model', providing
371 task-relevant social information to a naïve observer before they perform the same task, with
372 the latter then acting as the model to a new individual in the chain, and so on (Whiten &
373 Mesoudi, 2008). Using this method, baboons were given a pattern recognition task in which
374 the output of the previous participant formed the stimuli for the following participant in the
375 chain, and so on (Claidière et al., 2014, also see Saldana et al., 2019). Over time, pattern
376 reproduction improved (increased performance, criterion (iii)) as there emerged structure in
377 the lineages and across 'generations', similar to how human languages evolve (Kirby et al.,
378 2008). Importantly, repeated exposure to one's own learning output did not yield the same
379 level of change, suggesting that chains comprising of different individuals were responsible
380 for improving the learnability of the task (meeting criterion (iv)).

381

382 Similar improvements across transmission chains have been reported in homing pigeons
383 (*Columba livia domestica*), where the homing routes of birds later in chains were more
384 efficient than earlier 'generations' and solo individuals (Sasaki & Biro, 2017). 'Generational'
385 change was explored by first pairing a bird with an established homing route with a naïve
386 flight partner. Once this naïve partner had flown with their partner, they became the

387 experienced participant paired with the next naïve subject in the chain, until five successive
388 generations were formed. Birds in the transmission chain showed measurable improvements
389 in their routes, such that the fifth generation's routes were 1.2 km shorter than those of the
390 first-generation (meeting the extended criterion of generational improvements). This
391 improvement over time was also more pronounced than for solo birds repeating the same
392 number of flights, which produced only a 0.05 km reduction in their route - therefore meeting
393 criterion (iv).

394
395 Improvements in behavioural efficiency have also recently been documented in great tits
396 (*Parus major*) using the 'replacement' method. This method is similar to transmission chains
397 except each generation is a group of individuals instead of a dyad (Chimento et al., 2021).
398 Here, birds could gain a reward by either pushing open a door in a demonstrated but
399 inefficient direction, or they could innovate the efficient, quicker alternative by pushing the
400 door from the opposite side. For birds that were in the 'static' control condition, repeatedly
401 testing the same groups birds, the efficient behaviour was discovered (easily invented, thus
402 not meeting criterion (iv)) but was not widely adopted. For the birds in the 'turnover'
403 condition, repeatedly replacing two of the six birds in each 'generation' with naïve ones, the
404 efficient alternative was not just invented (criterion (i)) but also widely adopted (social
405 transmission: criterion (ii) and improvement (iii)). Thus, naïve birds appeared key to
406 populations' transition to the improved (quicker) solution by overcoming experienced
407 individuals' tendency to stick with their practiced methods (Chimento et al., 2021).

408
409 As transmission chains and the replacement method are usually not feasible with
410 chimpanzees (discussed in detail below), recent studies have employed 'closed group' or
411 'open diffusion' task designs (Whiten & Mesoudi, 2008). Typically, these tasks involve
412 training a chimpanzee on a behavior that subsequently serves as a model to the rest of their
413 group. Davis et al. (2016) tested whether groups of chimpanzees would relinquish a
414 practiced, inefficient solution for a more optimal (quicker) one introduced by a trained
415 demonstrator. As with Marshall-Pescini & Whiten (2008b), chimpanzees generally
416 perseverated on their inefficient behaviors, and only switched to the more efficient behavior
417 when their practiced technique became almost impossible to perform (see also Harrison &
418 Whiten, 2018; Hopper et al., 2011; Hrubesch et al., 2009; Manrique & Call, 2011, but see
419 Jacobson & Hopper, 2019). This indicated a degree of conservatism in chimpanzees, similar
420 to that observed in great tits (Chimento et al., 2021), where known behaviors interfered with
421 the adoption of an alternative, more efficient one that was shown to be within their ability to
422 invent (Davis et al., 2016; not meeting criterion (iv)). Further investigation indicated that
423 behavioral flexibility was linked to the solution complexity and payoff incentives, as
424 chimpanzees switched from a simple, known behavior to a newly observed and better paying
425 solution of equal difficulty, but more rarely relinquished known behaviors when they were
426 complex or were of similar difficulty but not higher paying (Davis et al., 2019). Abandoning
427 an act that may have taken considerable effort or practice to learn may show reluctance to
428 forgo well-rehearsed techniques or habits that were known to achieve a goal and may explain
429 behavioral stasis once a certain level of complexity is reached.

430
431 Similar closed group designs have been used to examine whether chimpanzees can socially
432 learn more complex (and efficient) solutions from a conspecific demonstrator (Vale, Davis, et
433 al., 2017). Chimpanzees acquired behaviors that surpassed what individuals invented in the

434 absence of any social information (in comparable conditions). However, *groups* of naïve
435 chimpanzees appeared to pool their skills to discover the same behaviors. One individual
436 discovered part of the behavioral sequence of interest (unscrewing a stop valve to make a
437 functional straw), before a second individual used their discarded tool to obtain a juice
438 reward; a sequence that spread to others albeit at a slower rate and attained by fewer
439 individuals than occurred in the model seeded groups. These data therefore only provide
440 suggestive evidence for cumulative advancements in this technological (tool deconstruction)
441 task as the role of social learning was not clear cut (criterion (ii)). The same population of
442 chimpanzees was recently tested on a task that afforded participants to construct, rather than
443 deconstruct, tools to gain progressively valuable rewards (Vale et al., 2020). The complexity
444 of solutions observed in groups did not surpass those discovered by chimpanzees tested
445 individually indicating a lack of CCE (not meeting criterion (iv)). The differences in findings
446 across studies maybe be explained by the type of tool modifications involved (i.e.,
447 construction/deconstruction), a point we discuss in more detail below.

448

449 *Chimpanzee invention*

450

451 Whether the complex behaviors observed in wild populations are cumulative has also been
452 tested by exposing naïve, captive populations to the ecological conditions thought to be
453 necessary for the behavior to occur. The logic is that if animals discover the same behaviors
454 as their wild counterparts, we can conclude that (i) action copying was not necessarily
455 required for the inception of the behavior and (ii) it does not surpass an individual's capacity
456 to develop through personal exposure to the right conditions. This work, by Tennie and
457 colleagues, has focused on several wild chimpanzee tool use behaviors, including pestle
458 pounding, algae scooping, and nut-cracking (Bandini & Tennie, 2017, 2019, 2020; Neadle et
459 al., 2020). In all cases except nut cracking, chimpanzees were able to re-invent the behavior
460 under the conditions provided in captive settings, suggesting they are within an individual's
461 capability to invent (their 'Zone of Latent Solutions' or 'ZLS', Tennie et al., 2009, 2016).

462

463 There are several challenges to the ZLS, however. It is difficult to be certain that these
464 animals, some of whom were wild born, were truly naïve to these behaviors - the researchers
465 rely upon keeper and caretaker testimony to document the animals' experience (Bandini &
466 Tennie, 2017). A further concern is the omittance of complex components of these behaviors
467 that are typically needed in the wild. For example, the processes of finding, selecting, and
468 fashioning the correct tool for the task are not typically required in captive tasks, where the
469 chimpanzees are instead provisioned with useable tools from the outset (Bandini & Tennie,
470 2017). Notably, the objective of the task was to re-create the *act*, as a test for the role of
471 form-copying in the examples from wild chimpanzees and did not claim to be re-creating the
472 entire behavior. For example, in an 'algae scooping' study, chimpanzees were provisioned
473 with a stick to fish a floating piece of bread out of water, whereas in the wild, chimpanzees
474 must first identify an appropriate stick (smooth or hooked) of adequate length, detach it, and
475 even modify it by the removal of smaller branches or fraying the ends (Boesch et al., 2017).
476 Thus, while these studies suggest that at least some components of these behaviors exist in a
477 ZLS, we encourage future studies to examine whether whole behavioral sequences can be re-
478 invented, rather than just part of the action.

479

480 Research on CCE in nonhuman animals both from the wild and captivity is suggestive,
481 however, it is not *conclusive* evidence of CCE. At present, notwithstanding evidence in non-
482 primate species that we discuss further below, one of the most convincing cases from wild

483 data is chimpanzee nut-cracking. This is because it can take years to master (Inoue-Nakamura
484 & Matsuzawa, 1997), is not easily re-invented by naïve individuals (Needle et al., 2020), and
485 involves social learning (Marshall-Pescini & Whiten, 2008a). However, chimpanzees have
486 been cracking nuts for thousands of years (Mercader et al., 2007) which raises questions over
487 whether improvement has been made to this behavior - over millennia. Nevertheless, the
488 behavioural change that might have predated the available archaeological record is also
489 unknown (Whiten, 2021). Researchers working with captive populations, or performing field
490 experiments, have documented improvements in behavioral efficiency across transmission
491 chains of multiple participants (Chimento et al., 2021; Claidière et al., 2014; Sasaki & Biro,
492 2017). Open diffusion experiments have also begun to show promise as a way to assess CCE,
493 revealing modest increases in behavioral complexity (Vale et al., 2017, but see Vale et al.
494 2020), and have created the opportunity to isolate some of the socio-cognitive factors that
495 may play a role in species' extent for CCE (Davis et al., 2016; Dean et al., 2012). Many of
496 these studies have also highlighted some of the difficulties of studying CCE and associated
497 methodological limitations they can impose in nonhumans (a subject discussed later),
498 including assessment of CCE in non-primates.

499

500 *Cultural evolution and CCE in animal song*

501

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

508

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

527

528 Song development in zebra finches has been tracked using similar experimental methods
529 used to study CCE in humans. Typically, young male zebra finches learn their song by
530 copying adult males (criterion (ii)), developing wild-type, local variants, with some

531 individual variability (indicative of criterion (i)). When deprived of this experience, however,
532 young males develop a distinguishable, relatively unstructured ‘isolate’ variant, allowing
533 song ‘recovery,’ or development, to be traced. Fehér et al. (2009) paired juveniles finches
534 with isolate ‘tutor’ birds, before placing learners in transmission chains (pupils became the
535 tutors for the next generation and so forth). Similar to whale song, finches’ songs changed
536 over learning events, recovering from isolate versions as similarity to the wild variant
537 increased in just a few generations (suggestive of (iii), but unknown if wild-type song
538 represents an improvement). Furthermore, songs of later generations differed from the isolate
539 songs, which is indicative of CCE (criterion (iv)). These findings mirror results from
540 transmission chain studies with human spoken language, where learnability and structure
541 improve with iterated learning events between individuals (Kirby et al., 2008).

542

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

547

Study	Species	Observed behavior	Wild/captive/field experiment	Core criteria				Extended criteria
				Invention (Criterion (i))	Social transmission (ii)	Measurable improvement (iii) through (i & ii)	Exceeds individuals' discoveries (iv)	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>)	Puzzlebox: two levels of efficiency	Captive	✓	✓	✓	x	✓
Claidiere et al. (2014)	Baboons (<i>Papio papio</i>)	Memorizing patterns on touchscreens	Captive	✓ - Change through transmission error	✓ - No social interaction, but met social learning definition of learning from 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>)	Puzzlebox: two levels of increasing efficiency	Captive	Invention model seeded	✓	✓	x	x
Davis et al. (2019). Study 2.1	Chimpanzees (Pan troglodytes)	Puzzlebox: two levels of increasing complexity	Captive	Invention model seeded	✓	✓	x	x
Dean et al. (2012)	Children, chimpanzees & capuchins (<i>Homo sapiens</i> , <i>Pan troglodytes</i> , <i>Cebus apella</i>)	Puzzlebox: three levels of increasing complexity	Captive	✓	?	✓ - But only children reached hardest level	x - Reindl et al. (2020)	x
Feher et al. (2009)	Zebra Finches (<i>Taenyopygia guttata</i>)	Song structure	Captive	✓	✓	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 (though Allen et al. 2018 document changes in complexity)	x	✓ Repeated change over 11 years

Garland et al. (2017)	Humpback Whales (<i>Megaptera novaeangliae</i>)	Song structure	Wild	✓	✓	x	x	x
Hunt & 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	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 spp.</i>)	Transporting objects	Captive	✓	✓	✓	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 & 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 & Whiten (2008a)	Chimpanzees (<i>Pan troglodytes</i>)	Nut-cracking	Captive	Invention model seeded & one chimpanzee showed the behavior, thought to be due to past experience	✓	x	x	x
Marshall-Pescini & Whiten (2008b)	Chimpanzees (<i>Pan troglodytes</i>)	Puzzlebox: two levels of increasing complexity	Captive	✓	✓ - 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	Invention model seeded & invention in controls	✓	✓	x - Discovered by individuals with no social demonstrations	x
Sanz et al. (2009)	Chimpanzees (<i>Pan troglodytes</i>)	Chimpanzee termite fishing	Wild	x	C - Probable but no direct evidence	✓	x	x
Sasaki & 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. (2020)	Chimpanzees (<i>Pan troglodytes</i>)	Tool use and tool modification task	Captive	✓	C - Probable transmission of simple, but not complex techniques	x	x	x
Vale et al. (2017)	Chimpanzees (<i>Pan troglodytes</i>)	Complex tool behavioral sequence	Captive	Invention model seeded & invention in a non-seeded group	✓	✓	✓ - But partial discovery in asocial control individual	x
Williams et al. (2013)	Savannah Sparrows (<i>Passerculus sandwichiensis</i>)	Song segments	Wild	x	✓	✓	x	✓
Yamamoto et al. (2013)	Chimpanzees (<i>Pan troglodytes</i>)	Extracting juice from container	Captive	✓	✓	✓	x	x

548

549

550

551 *Table 1:* Studies of potential CCE in nonhuman animals against our proposed criteria. ✓ denotes meeting the criterion, x denotes failing to meet
552 criterion and C denotes circumstantial or indirect evidence of meeting the given criterion.

553 **Evaluation of the methods and advancements**

554

555 Despite the significant advances made over the past two decades, limitations remain for
556 comparative research in terms of what can or cannot be assessed with nonhuman animals and
557 their implications for CCE research. Specifically, issues concerning sample sizes, species
558 comparability of motor and cognitive abilities, as well as participant demographics which
559 may require addressing for the field to continue to move forward. We next describe these
560 concerns and provide some suggestions for their resolution.

561

562 *Sample sizes*

563

564 Accessing sufficient sample sizes (comparable to human research) is difficult when studying
565 many nonhuman animal species (Sjoberg, 2017). Research facilities, sanctuaries, and zoos
566 often have limited physical spaces and/or facilities, and ethical guidelines, correctly,
567 encourage reducing the number of tested nonhuman animals to the smallest possible number.
568 This means the number of social groups, as well as the size of social and asocial samples are
569 limited to relatively small numbers, and often participants have been subject to similar
570 studies before (meaning they are not experimentally naive). In no small part because humans
571 are detrimentally impacting nonhuman primate population numbers and behavioural diversity
572 (Estrada et al., 2017; Kühl et al., 2019), there are similar sample size issues in the wild, where
573 accessing and/or accurately tracking animals (or species) can be logistically difficult. The
574 power to statistically detect effects is therefore difficult - particularly when using multiple
575 comparisons - and generalizability of findings is weakened. Although concerns regarding
576 replicability have led to many disciplines addressing issues of sample sizes (Loken &
577 Gelman, 2017), tackling this in some comparative research is not easily solved given
578 generational and/or multi-group studies demands relatively large sample sizes and many
579 species of interest are not available in such numbers.

580

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

595

596 *Motor and cognitive abilities*

597

598 A key methodological concern for any comparative study is to develop tasks that capture
599 appropriate contextual validity for the species being examined. Multiple factors need to be
600 considered, including whether study species have appropriate motor and cognitive capacities
601 concerning administered tasks. Designing experimental paradigms, tasks, and apparatuses

602 that allow direct comparisons across animal species means considering whether specific
603 actions are more difficult for one species than for another.

604

605 Tool use and puzzlebox tasks for CCE research have allowed researchers to make direct
606 (Dean et al., 2012; Tennie et al., 2009) and indirect (Davis et al., 2016; McGuigan & Whiten,
607 2009; Reindl et al., 2016; Whiten, 2017b) inferences regarding the socio-cognitive
608 mechanisms underpinning CCE in humans and chimpanzees. An important consideration,
609 however, is whether the level of dexterity required for task success is more or less
610 challenging for a given species. Motor diversity is a key predictor of innovative and
611 individual problem-solving abilities in birds, nonhuman primates, and children (Diquelou et
612 al., 2016; Griffin et al., 2014; Griffin & Guez, 2014; Keen, 2011), and thus species
613 differences in this domain may limit any potential comparative conclusions. Tasks that
614 require fine motor skills, for example, may be better suited to humans than to other animals
615 or may require a substantial period of training for nonhuman animals to reach required
616 criteria (Davis et al., 2019; Vale, Davis, et al., 2017). If significant training is required, this
617 may also weaken comparisons to human studies in which participants require far less training
618 for similar tasks. Animals learning tasks can also be required to observe humans (i.e., a
619 heterospecific) face to face, requiring copying mirror images, while children are often
620 adjacent to (i.e., a conspecific) experimenters, meaning they can use motor imitation.

621

622 Relatedly, the type of actions we ask of animals may have important implications for the
623 study of CCE. For instance, deconstructing tools may be more species-appropriate, and
624 ecologically valid than constructing ones for tool-using species (Bania et al., 2009). This is
625 because in the wild animals' tools are typically made and modified using broadly destructive,
626 rather than constructive, actions, such as detaching probe sticks or leaf tools, and trimming
627 them (e.g., chimpanzees: (Boesch et al., 2017; bearded capuchin monkeys: Mannu & Ottoni,
628 2009; New Caledonian crows: Hunt & Gray, 2003). At our study site, the National Center for
629 Chimpanzee Care (NCCC), individuals also fashion tools by detaching materials with greater
630 ease than those that require combinatory actions, suggesting that this is not simply an artifact
631 of what is readily available in the wild. In the first tool construction task conducted at this
632 site, fourteen of 50 chimpanzees fashioned elongated tools by inserting one tool component
633 into another (Price et al., 2009). However, very few chimpanzees beyond these have since
634 demonstrated such skills, despite testing nearly the entire colony on various construction
635 tasks (Neldner, 2020; Vale et al., 2016; Vale et al., 2020, Vale et al., unpublished data). For
636 example, only three of 20 naïve chimpanzees recently tested on tool construction learned how
637 to combine tools and they failed to use them as a functional tool to gain out-of-reach rewards
638 (Vale et al., 2016). Learning to deconstruct object components to make a functional tool, or
639 for exchange for higher valued rewards, in contrast, have been relatively prevalent in our
640 colony (Neldner, 2020; Vale, Davis, et al., 2017; Vale et al., unpublished data). Creating
641 tasks that are species-appropriate is therefore essential to avoid concluding that species lack
642 certain skills when the outcome may be an artifact of specific task conditions (F. B. M. de
643 Waal, 2016; Leavens et al., 2017).

644

645 Breeding in captive chimpanzee populations has been banned in the U.S. (and several other
646 countries) since 2007 (Knight, 2008), meaning populations in many locations are aging and
647 there are very few juveniles or young chimpanzees available for testing. When dealing with
648 many aging captive nonhuman primate populations, we must consider the effects of their
649 cognitive abilities, motivation, and participation in experiments that vary across the lifespan,
650 as these will ultimately have consequences on the conclusions we draw. Whether animals
651 attempt and persist at tasks, for example, can decline with age (Barbary macaques, *Macaca*

652 *sylvanus*: Rathke & Fischer, 2020), while perseveration with known solutions or strategies
653 can increase (rhesus macaques: Lai et al., 1995: for examples of aging and cognitive decline
654 in other species, see Chapagain et al., 2020 for dogs; Kapellusch et al., 2018 for rats and
655 Kwapis et al., 2020 for mice). Openness, linked with cognitive performance, also changes
656 over the chimpanzee lifespan – with males in particular decreasing over adulthood (Rawlings
657 et al., 2020). Candidate CCE behaviors such as nut cracking are cognitively demanding and
658 can take years to master, and if aging populations are showing cognitive decline these factors
659 will have significant implications for studies of animal learning. CCE requires behavioral
660 change, individual or group level behavioral flexibility and the motivation to learn often
661 complex new skills, and this may lead researchers to underestimate species' CCE abilities.

662 663 *Sampling biases*

664
665 A decade ago, psychologists acknowledged an overreliance on so-called WEIRD (Western,
666 Educated, Industrialized, Rich, and Democratic) (human) samples, who often perform at the
667 extreme ends of continuums of psychological studies (Henrich et al., 2010). The pace of
668 human cross-cultural research has rapidly increased over recent years - including within the
669 field of CCE. As a result, the field has made and continues to make, significant conceptual,
670 theoretical, and methodological improvements through the assessment of diverse populations
671 (Broesch et al., 2020; Hruschka et al., 2018; Kline et al., 2018; Nielsen et al., 2017). A
672 similar argument regarding nonhuman animal samples was raised at the same time where
673 individuals raised in captivity (i.e. Barren, Institutional, Zoo, And other Rare Rearing
674 Environments - BIZARRE) may not represent their wild counterparts (Leavens et al., 2010).
675 Yet, comparative research has yet to fully address the issue of sampling biases (Webster &
676 Rutz, 2020), where individual and group level factors impact which species and participants
677 engage in behavioral research. Despite extensive and valuable investment in studying wild
678 populations, sampling biases have important implications for the generalizability of data and
679 conclusions that can be drawn from CCE studies.

680
681 At the individual level, factors such as personality, dominance status, prior testing
682 experience, social status, and rearing history are important causes of selection bias (Altschul
683 et al., 2017; Brosnan et al., 2015; Herrelko et al., 2012; Hopper et al., 2014; Morton et al.,
684 2013; Rawlings et al., 2020). Much of primate behavioral research is based on voluntary
685 participation, for good reason, but this also means that individuals who enjoy testing and/or
686 are high ranking enough are most likely to participate, and indeed are those as trained
687 demonstrators – which impacts subsequent learning of behaviours in groups (Kendal et al.,
688 2015; Vale et al., 2020; Watson et al., 2017). At the group level, nonhuman animals raised in
689 captive contexts may not be representative of the species at large. Frequent caregiver
690 interaction and exposure to enrichment activities or behavioral testing may skew behaviour
691 and task performance, as does interaction with tasks through bars, making comparisons with
692 wild or even other captive populations and children difficult (Haslam, 2013; Leavens et al.,
693 2017). Conversely, captive environments are comparatively impoverished as a function of
694 less stimulation, contextual diversity, and fewer group members, compared to natural
695 conditions (Boesch, 2007). Further, in many research sites, nonhuman primate groups have
696 been rearranged or moved locations, which can have a significant impact on social bonds and
697 social-based research (Dufour et al., 2011; Schel et al., 2013), as can environmental
698 uncertainty (Galef & Whiskin, 2004). Implementing steps to overcome selection bias is
699 crucial for a fairer representation of the population intended to be examined (Morton et al.,
700 2013; Webster & Rutz, 2020).

701
702 Here we reiterate the recent STRANGE framework proposed by Webster and Rutz (2020)
703 which provides an assessment tool that researchers can use to identify if their sample is
704 representative of the larger population of interest. Seven categories are identified, namely
705 subject's: Social background; Trappability and self-selection; Rearing history; Acclimation
706 and habituation; Natural changes in responsiveness; Genetic make-up; and Experience (i.e.,
707 STRANGE). These categories highlight, for example, that some individuals may be more
708 motivated to participate than others ('Trappability and self-selection') and more or less likely
709 to solve particular tasks depending on their previous 'Experience' and 'Rearing' conditions.
710 Researchers interested in CCE may find this a useful framework to assess samples'
711 representativeness and how it may be improved. For example, self-selection biases may be
712 reduced by testing social groups, and for extended periods to overcome potential task
713 monopolization, or by introducing multiple tasks or stimuli so that more than one subject can
714 participate at any given time. Variation in subject rearing histories and experimental
715 experience, if known, can also be controlled for either statistically or in the research design
716 (Bandini, 2021; Neadle et al., 2020; Vale et al., 2020). Implementing comparable testing setups
717 between species will also allow for fairer comparisons (McGuigan et al., 2017; Neldner, 2020).
718

719 The STRANGE framework is therefore a useful tool for researchers to present information
720 about their study group which allows fairer conclusions on the generalizability of the
721 findings. We also fully acknowledge it is not always possible to control the fact that a sample
722 is STRANGE. Work on such samples has provided a wealth of key knowledge on the
723 evolutionary basis of CCE, and with breeding bans across many institutions, nonhuman
724 primate researchers are running out of opportunities to collect such data. We suggest in such
725 cases that comparative researchers fully and openly acknowledge the sample biases. Doing so
726 will avoid the extreme data collected from STRANGE samples to become interpreted as the
727 default of the entire species.
728

729 Likewise, comparisons between the cultural learning strategies of human children and
730 nonhuman animals have been a valuable line of research for establishing the ontogeny of
731 CCE (Dean et al., 2012, 2014; Tennie et al., 2009; Vale, Flynn, et al., 2017). Yet, as with
732 primates, while the field is beginning to assess diverse populations, the vast majority of
733 experimental CCE research on children has been on WEIRD populations. This bias presents
734 issues with conclusions that can be drawn when comparing children's performance with other
735 species, and researchers should be mindful of the human population in which they study.
736 Tools such as STRANGE frameworks could usefully be applied to developmental research to
737 improve assessment of the generalisability of findings, which may also have similar biases
738 within populations. Children who have caregivers who actively consent to participate in
739 scientific studies, and children who willingly participate in research, for example, can
740 generate selection biases (Anderman et al., 1995). As with nonhuman animal studies, we
741 encourage CCE researchers interested in development to evaluate, report and improve the
742 representativeness of their samples.
743

744 *The value of observational and experimental approaches* 745

746 While much of our focus has been on experimental work, our intention is not to prioritize this
747 method over observational approaches. Experiments are not feasible with certain species
748 (e.g., large animals such as whales, Janson & Brosnan, 2013), and can lack external validity.
749 Observational approaches, by contrast, afford documentation and evaluation of naturally
750 occurring candidate CCE behaviours (Henrich, 2015; Noad et al., 2000; Reyes-García et al.,

751 2016), which can be highly informative of species' natural behaviors as well as for planning
752 experiments. The use of both approaches is required to make crucial, and complementary,
753 contributions to the field of comparative CCE.

754

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

771

772 The continued use of field experiments, alongside other experimental and observational
773 approaches, will be crucial to documenting the scope of CCE in the animal kingdom in ways
774 not previously possible. The development of sophisticated technology and advanced
775 methodological approaches are providing new methods to collect rich data on CCE in diverse
776 species. Lightweight trackers and camera traps have allowed researchers to detail migration
777 routes and improvements in spatial navigation in wild animals. Advanced statistical
778 approaches, such as network-based diffusion analysis (NBDA), mean that scientists can
779 document the advent and spread of innovations across dynamic social networks (Allen et al.,
780 2013; Hobaiter et al., 2014; Migliano et al., 2020; Wild et al., 2019). Such tools will be
781 valuable for understanding how the social environment impacts CCE in natural conditions.

782

783 In humans, the vast majority of evidence for CCE in non-western populations remains based
784 on ethnographic data (Henrich, 2004; Reyes-García et al., 2016; Salali et al., 2016), which is
785 problematic from the perspective of understanding other species' CCE because these results
786 are not comparable to those generated in lab and field experiments or observational research
787 in non-human species. Fortunately, the recent growth of cross-cultural research means that
788 mechanisms such as social learning and innovation are being studied experimentally in a
789 broader range of populations (Berl & Hewlett, 2015; Clegg et al., 2017; Legare, 2017;
790 Neldner et al., 2017; Nielsen et al., 2014; Rawlings et al., 2019). We encourage cross-cultural
791 research to complement ethnographic studies with explicitly experimentally CCE research in
792 diverse populations, using ethical and equitable approaches (Broesch et al., 2020; Urassa et
793 al., 2021). Additionally, we simultaneously encourage cross-cultural researchers to validate
794 experimental tasks and paradigms to improve construct validity and thus quality of
795 explanations (Broesch et al., 2020; Hruschka et al., 2018; Kline et al., 2018; Lew-Levy et al.,
796 2020). These steps will be essential to for improving our understanding of how cultural
797 diversity shapes the remarkable diversity of human CCE and how CCE evolved in humans
798 and other species.

799

800 *Directions for future research*

801
802 We next discuss two key areas we believe are particularly pertinent to continuing to move the
803 field of cumulative cultural evolution forward. We suggest that refining asocial control
804 testing methods and continuing to broaden study species will be particularly beneficial for
805 improving theory in future research.

806
807 *Asocial control testing methods*

808
809 Crucial to advancements in the field of CCE include the addition of asocial controls that
810 examine an individual's invention abilities, to provide a comparator for group-level
811 achievements and transmission chain designs that allow 'generational' changes to occur
812 across participants (Miton & Charbonneau, 2018; Reindl et al., 2020). For nonhuman animal
813 research, however, these require individuals to be separated from their group, which may be
814 undesirable for a social species and is not always possible for many species (particularly into
815 individual isolation). Individuals may be reluctant to separate or testing facilities may have
816 regulations on whether, and for how long individuals can be separated, and isolation can
817 induce unnecessary stress upon participants (which can also reduce their willingness to
818 participate or change their behavior). Transmission chain studies, which involve dyadic
819 testing, require careful consideration of differences in dominance statuses between pairs of
820 individuals. Moreover, researchers rarely consider wider contextual issues when comparing
821 asocial to group performance. Individuals in asocial conditions may show increased vigilance
822 compared to those in groups, and they lack opportunities for social facilitation that enhances
823 activity based on the mere presence of others (Zajonc, 1965). Recent research shows that
824 chimpanzees tested in social groups exhibit more diverse behavioral repertoires and had
825 greater task success than participants tested in the absence of conspecifics (Vale et al., 2020).
826 This suggests that social facilitatory effects and/or a larger pool of skills and motivations in
827 groups can influence study results and that social settings should be considered by
828 researchers as they design control conditions (see also Finestone et al., 2014).

829
830 These issues can prohibit researchers from using certain techniques or result in unbalanced
831 study designs, where, for example, few individuals form the asocial controls (or come from
832 smaller groups) compared to much larger social groups. Though this is often necessary, it is
833 problematic as we often do not know if individuals would reach the same solutions as groups
834 can if given the same cumulative exposure time or if more control individuals were tested
835 (see Table 1).

836
837 One potential solution is to test individuals in the presence of others (either in dyads or
838 groups, although dyadic testing faces similar separation and dominance issues as
839 transmission chain studies). Similar to asocial controls, such naïve groups can provide
840 baselines for groups that are seeded with animals trained on complex or efficient solutions,
841 although this method does not work as a comparator for unseeded groups. Dyads and control
842 groups may also benefit from social facilitation, as well as reduced vigilance, thereby ruling
843 this out as a potential explanation for any enhanced performance in experimental groups.
844 Alternatively, the role of social learning can be assessed even when control individuals
845 necessarily receive shorter task exposure than groups, by controlling for test times or the
846 number of trials participants engage in. That is, if groups are tested for longer periods or
847 receive more trials, their data can be capped so they are equivalent to asocial control
848 durations. A note of caution is required with this later method, as researchers will need to
849 ensure they provide a reasonable amount of time for subjects to develop the skill or behavior
850 of interest.

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Age differences in comparative studies

Studies directly comparing humans and chimpanzees have been highly informative for our understanding of what socio-cognitive 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., 2020; 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 socio-cognitive tasks, and thus using young children allows us not to conflate species differences in CCE behaviours with inter-species 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 puzzleboxes, 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 and chimpanzees' cultural learning strategies. In non-human primates, surveys suggest that adults are more innovative than nonadults (Reader & Laland, 2001). Observational studies have shown that infancy and juvenility maybe be a sensitive period chimpanzees to socially acquire complex cultural behaviours, such as nut cracking (Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2017; Lonsdorf et al., 2004). Likewise, young children are particularly reliant on copying others, but 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 non-human 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, as this population is heavily biased towards 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 US), 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 collaborative 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 on 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 behaviours, and the maximum level of complexity or efficiency reached would allow for adult comparisons of both species.

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902

903 *Broadening study species*

904

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

918

919 Studying other species is critical to gain a richer understanding of nonhuman behavior,
920 however, taxa such as birds or bumblebees also offer some methodological advantages over
921 nonhuman primates. Logistically, it may be easier to recruit larger sample sizes and/or
922 implement generational study in smaller-bodied and/or shorter-lived species. It may also be
923 easier to make use of natural behaviors with certain species (such as songs or migration
924 routes), which improves ecological validity. In addition, the greater variety of natural
925 behaviors available across the entire animal kingdom increases the number of questions that
926 can be answered relative to studying only primates. For instance, we can ask is CCE more
927 common in material culture or communication? Is it more common in long-lived organisms
928 in which individuals have extensive opportunities to learn from one another, or in shorter-
929 lived organisms in which there may be particular advantages to learning from others? As we
930 continue to diversify our study species these questions can be addressed, and in turn, more
931 questions will emerge.

932

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

941

942 Perhaps most critically, throughout comparative psychology there is a bias towards assuming
943 that multi-step and/or highly social behaviors, like CCE, are complex and therefore require
944 large brains, an assumption that has repeatedly been proven false (e.g., empathetic
945 responding in rats; Bartal et al., 2011; interspecific cooperation in moray eels and grouper;
946 Bshary et al., 2006; and visual individual recognition in wasps; Tibbetts, 2002). Knowing
947 which species show aspects of CCE, and how it may vary across organisms, is required to
948 both fully understand what behavioral mechanisms are essential and to better understand
949 extant variability. For example, there are clear differences in what can be accomplished by

950 humans with language, and chimpanzees without, but language obscures other less obvious
951 factors; studying the variability in other species helps identify how these factors shape CCE
952 as well.

953

954 **Concluding remarks**

955

956 The cumulative nature of human culture is unquestionably distinct from all other species, yet
957 the question of nonhuman animal CCE remains an open one. The marked increase in CCE
958 research, both within the primates and more broadly across species, over the last two decades
959 has significantly improved our understanding of its cognitive underpinnings, its ontogenetic
960 and evolutionary origins, and the extent to which it exists outside of humans. Comparative
961 research has been crucial to identifying cross-species similarities and differences in cultural
962 behaviors and, ultimately, to identify key mechanisms underpinning the uniqueness of human
963 cumulative cultural evolution. As the field has developed, however, researchers have used
964 different criteria to determine CCE, which has led to studies that are not directly comparable.
965 The field of primatology has critically improved our knowledge of CCE through the
966 collection of data from multiple sites both in captivity and in wild settings and longitudinally.
967 Yet it also suffers from small samples, making generalizability difficult, and primates are
968 long-lived organisms for which generational studies are nearly impossible. We propose that a
969 combination of stricter definitions, more robust methods and a broader phylogenetic scope
970 will allow us to more fully understand the evolution and development of CCE and, therefore,
971 better understand what, if any, aspects of it are unique to humans and how our behavior fits
972 into that of the rest of the animal kingdom.

973

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