The Method of Local Restriction: in search of potential great ape culture-dependent forms

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ABSTRACT

Humans possess a perhaps unique type of culture among primates called cumulative culture. In this type of culture, behavioural forms cumulate changes over time, which increases their complexity and/or efficiency, eventually making these forms culture-dependent. As changes cumulate, culture-dependent forms become causally opaque, preventing the overall behavioural form from being acquired by individuals on their own; in other words, culture-dependent forms must be copied between individuals and across generations. Despite the importance of cumulative culture for understanding the evolutionary history of our species, how and when cumulative culture evolved is still debated. One of the challenges faced when addressing these questions is how to identify culture-dependent forms that result from cumulative cultural evolution. Here we propose a novel method to identify the most likely cases of culture-dependent forms. The ‘Method of Local Restriction’ is based on the premise that as culture-dependent forms are repeatedly transmitted via copying, these forms will unavoidably cumulate population-specific changes (due to copying error) and therefore must be expected to become locally restricted over time. When we applied this method to our closest living relatives, the great apes, we found that most known ape behavioural forms are not locally restricted (across domains and species) and thus are unlikely to be acquired via copying. Nevertheless, we found 25 locally restricted forms across species and domains, three of which appear to be locally unique (having been observed in a single population of a single species). Locally unique forms represent the best current candidates for culture-dependent forms in non-human great apes. Besides these rare exceptions, our results show that overall, ape cultures do not rely heavily on copying, as most ape behaviours appear across sites and/or species, rendering them unlikely to be culture-dependent forms resulting from cumulative cultural evolution. Yet, the locally restricted forms (and especially the three locally unique forms) identified by our method should be tested further for their potential reliance on copying social learning mechanisms (and in turn, for their potential culture-dependence). Future studies could use the Method of Local Restriction to investigate the existence of culture-dependent forms in other animal species and in the hominin archaeological record to estimate how widespread copying is in the animal kingdom and to postulate a timeline for the emergence of copying in our lineage.

Key words: cumulative culture, culture-dependent forms, great ape behaviour, latent solutions, copying, locally restricted forms, locally unique forms

CONTENTS

I. Introduction ................................................................. 1442
II. Defining ape cultures ....................................................... 1443
III. Charting differences in form frequencies: the method of exclusion ......................................................... 1445
   (1) Tool use and food processing ........................................... 1445
   (2) The gestural domain ..................................................... 1446
   (3) The vocal domain ....................................................... 1447
   (4) Why a new method (the Method of Local Restriction) is required ................................................................. 1448
IV. Locally restricted forms remain undetected by the method of exclusion ......................................................... 1448
V. Applying the method of local restriction: in search of potential great ape culture-dependent forms ........ 1449
   (1) Results of the Method of Local Restriction ......................................................... 1450

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I. INTRODUCTION

Social learning in general refers to behaviours that are influenced by the interaction with other individuals or their products (Galef, 1983). A sub-type of social learning, form-copying (henceforth copying or copying social learning), takes place via mechanisms that allow the detailed acquisition of behavioural forms (here encompassing bodily actions as well as artefacts). Copying social learning results in a measurable matched resemblance between the observed and learnt forms caused, at least in part, by the specific input form (Tennie, Hopper & van Schaik, 2020b). Copying mechanisms include processes such as the re-creation of physical actions themselves (often referred to as imitation) and the re-creation of artefact forms caused by the observation of these forms in a model [i.e. the re-creation of behavioural outcomes via emulation mechanisms such as end-state emulation (Whiten & Ham, 1992; Tomasello, 1996; Whiten et al., 2004)]. Moreover, actions and artefact forms can be recreated both on a one-to-one basis (including linear assemblages of items) and/or in hierarchically organised combinations (Tennie et al., 2020b).

Among primates, humans have been shown to heavily rely on copying mechanisms. As early as 18 months old, human children copy demonstrated physical actions even when these are causally irrelevant (Nielsen, 2006), a phenomenon that extends well into adulthood (McGuigan, Makinson & Whiten, 2011) and occurs cross-culturally (Nielsen & Tomaselli, 2010; Stengel, Hepach & Haun, 2020). Humans possess a perhaps unique type of culture based on and maintained by such copying variants of social learning known as cumulative culture (Tomasello, Savage-Rumbaugh & Kruger, 1993; Boyd & Richerson, 1996). Over time, cumulative culture produces behavioural forms that are copied by other, culturally connected individuals (Boyd & Richerson, 1996; Caldwell & Millen, 2009; Tennie, Call & Tomasello, 2009; Acerbi & Tennie, 2016; Heyes, 2018), leading to the transmission and maintenance of behavioural forms across generations. However, this transmission process is rarely perfect. Individuals that copy a behavioural form from models frequently modify the form introducing deviations (often due to copying errors; Eerkens & Lipo, 2005). In addition to copying deviations, changes in behavioural forms can also be introduced as intentional modifications, re-combinations and/or applications of pre-existing forms to novel contexts (Lewis & Laland, 2012). All these change-generating processes may affect the resulting behavioural forms’ complexity, efficiency or both. When the efficiency of these altered forms is (or it is perceived as) superior to that of pre-existing forms, these forms may be differentially retained in the population’s repertoire in a process known as the ratchet effect (Tomasello, 1999; Tennie et al., 2009). Where sufficient levels of copying fidelity are maintained, cumulative culture can theoretically be open-ended, meaning that forms can cumulate infinite changes over time (Lewis & Laland, 2012; Pradhan, Tennie & van Schaik, 2012; Tennie, Caldwell & Dean, 2018; but see Mesoudi, 2011). In addition, copying not only allows cumulated changes in behavioural forms but also the accumulation (increase in number) of behavioural forms per se (Dean et al., 2014).

Although we acknowledge the importance of other change-generating processes in cultural evolution as well as the role that innovations play in introducing novel substrates to which changes can be subsequently applied (either actively or via copying errors; Charbonneau, 2015), in this review we will focus on cumulated copying deviations (such as copying errors) on pre-existing forms. Copying deviations are a consequence of the repeated transmission of information via the copying social learning mechanisms supporting cumulative culture. Consequently, copying deviations are useful indicators that copying is involved in the acquisition of behavioural forms over time and across culturally unconnected populations.

The process of cumulative culture enables the cultural evolution of forms that eventually become ‘culture-dependent’ (Reindl et al., 2017; Tennie et al., 2018). Culture-dependent forms are behaviours that have cumulated changes over time (often differentially retained via the ratchet effect) and that cannot be re-innovated by a single, independent, individual without observing a model. Culture-dependent forms are causally dependent on the ability and application of copying, often due to their culturally evolved arbitrariness and/or complexity that leads to causal opacity (Gergely & Csibra, 2006). In humans, examples of culture-dependent forms that can only be acquired by copying knowledgeable models (or artefact samples) can be found across behavioural domains such as food processing.
techniques and recipes (e.g. Boyd, Richerson & Henrich, 2011; Henrich, 2017), rituals (e.g. Legare & Nielsen, 2015; Watson-Jones & Legare, 2016), dances (e.g. Laland, Wilkins & Clayton, 2016) and languages (e.g. LeMaster & Monaghan, 2007).

To illustrate the enormous quantity of culture-dependent forms included in human repertoires, consider how many distinct words exist across languages. Each word is a combination of sounds and written characters linked to an arbitrarily associated meaning (excluding onomatopoeias). The combinations of word meanings and pronunciations (forms) must be necessarily copied from experienced models and are therefore culture-dependent forms. Concentrating on word form itself, if we take the median of the number of words included in printed dictionaries of single languages (135000; sourced from Wikipedia) and we multiply this number by the approximate number of languages in the world (7000, www.ethnologue.com), we obtain a rough estimate of the number of existing culture-dependent words of about 945000000. Of course, this number is just a crude estimate and it would need to be adjusted by including languages without printed dictionaries and taking into account the overlap of word forms (e.g. homographs) and meanings (e.g. homonyms) within and across languages. However, even this rough estimate serves to visualise that if within just one human behavioural domain (language) there are already several million culture-dependent forms (words), the true number of human culture-dependent forms is likely to be measured in the billions across all human behavioural domains. Considering another example from the technological domain (patents), the United States Patent and Trademark Office has recently surpassed the 10 million mark, a useful proxy of the number of registered technological forms (source https://10millionpatents.uspto.gov). A fruitful future research avenue would be to systematically investigate the extent of behavioural form accumulation (i.e. number of behavioural forms; Dean et al., 2014) within and across human populations as well as across time.

Despite relying strongly on copying to acquire novel behavioural forms (Lyons, Young & Keil, 2007; Nia et al., 2015; Rawlings, Flynn & Kendal, 2017; Miu et al., 2018; Buckley, 2020), modern humans still learn some forms individually without the need to copy a model under certain circumstances, such as in simple tasks (Reindl et al., 2016; Neldner et al., 2020), when there is uncertainty about the quality of others’ information (Mesoudi, 2011) or given certain cue types (Legare et al., 2015). However, the relative contributions of these two mechanisms (individual learning and copying) to the formation of modern human repertoires remain strikingly different, with copying being considered by many as the secret of our species’ success (Boyd et al., 2011; Henrich, 2017; Tennie et al., 2020a; although see Sperber, 1996).

Whether non-human great apes possess culture-dependent forms is highly debated. This debate focuses on the issue that in order to develop culture-dependent forms, apes would necessarily have to be able to copy. Some previous studies have claimed that non-human great apes possess cumulative culture and culture-dependent forms (e.g. Boesch, 2003; Sanz, Schöning & Morgan, 2010; Yamamoto, Humle & Tanaka, 2013; Davis et al., 2016). Boesch (2003) proposed three behavioural forms (ectoparasite manipulation; digging of wells together with leaf sponge use and nut cracking) as purported cases of cumulative cultural evolution in chimpanzees. However, none of these behavioural forms has been conclusively shown to result from modifications successively cumulated onto ancestral form states (there is no evidence that they are the result of copying with modification) nor have their current forms been shown to rely on copying to be transmitted across individuals and generations (Tennie et al., 2009; Dean et al., 2014; Mesoudi & Thornton, 2018). Therefore, the behavioural forms proposed by Boesch (2003) do not actually fulfil the criteria to be considered culture-dependent forms. However, if we were to find at least one unquestionable culture-dependent form in modern non-human apes, this would have important implications for understanding when cumulative culture first evolved in the hominoid lineage. In particular, finding culture-dependent forms in non-human apes would support the possibility that the last common ancestor of apes and humans also possessed copying abilities and potentially cumulative culture [see Tennie et al. (2017) for a discussion of this debate]. In the following section we will describe the debate surrounding the underlying mechanisms of ape culture.

II. DEFINING APE CULTURES

Some of the classic definitions of culture exclude forms whose population patterns are not mediated by copying variants of social learning (Galef, 1990, 1992). For example, Galef (1992, p. 160) stated that non-human animals use social learning mechanisms “different from the behavioural mechanisms that underlie propagation of culture in humans”. Based on this view, Galef (1990, 1992) argued that animals do not possess culture, but rather what he labelled “traditions”. Galef proposed that these traditions were the result of other learning mechanisms, which are still social, but do not produce copies of behavioural forms. Non-form-copying social learning (henceforth non-copying social learning) can take place in non-observational and/or observational contexts [such as peering or begging (Jaeggi, van Noordwijk & van Schaik, 2008; Schuppli et al., 2016; Estienne et al., 2019; Musgrave et al., 2020)] and include learning mechanisms that transmit information other than behavioural forms themselves. That is, instead of transmitting know-how as copying does, non-copying social learning mechanisms transmit other types of knowledge, such as know-where, know-when, know-what, etc. (Bandini et al., 2020; Tennie et al., 2020a). Examples of non-copying social learning mechanisms are social facilitation (perhaps a variant of know-when), local enhancement (transmission of know-where), stimulus enhancement
(transmission of know-what) or learning about timing of events (transmission of know-when; for an overview of social learning mechanisms in general see Whiten, 2000). Although non-copying social learning mechanisms have measurable effects in the acquisition of know-how, they do not allow its direct transmission. Instead, non-copying social learning mechanisms generally lead to frequency increases (and subsequent stabilisation) of individually learnt behavioural forms (Bandini & Tennie, 2017; Tennie et al., 2009, 2020e).

In addition to non-copying social learning mechanisms, the expression of behavioural forms can be influenced by the social structure of a species (e.g. Lind & Lindenfors, 2010), environmental conditions (Sanz et al., 2014) and the existence of related forms in the repertoire that can downregulate behavioural frequencies via so-called conservatism (e.g. Hrubesch, Preuschoft & van Schaik, 2009).

Although there seems to remain a qualitative difference between human and ape cultures (Galef, 1992; Tomasello, 1999), both culture types are often equated in the literature (e.g. Whiten, 2011; Ramsey, 2013). Some authors have relabelled all social learning mechanisms as variants of copying even when forms are not actually copied (e.g. Laland, 2017). Others consider a species to have culture not based on its ability to copy, but on the number of traditions it shows (accumulation). Following this last criterion, any species with more than one tradition is defined to have culture (Whiten, 2005; Whiten & van Schaik, 2007). Still others focus on factors such as longevity or stability of behaviours, and grant cultural status to behaviours influenced by social learning that remain present after several generations (Whiten & van Schaik, 2007; Perry, 2009). In general, current definitions of animal culture often do not require evidence for the presence of copying social learning mechanisms.

Rather than focusing on the definition of culture itself and debating whether non-human species possess culture, we join the call of other cultural evolution researchers (e.g. Schuppli & van Schaik, 2019) to adopt a broad definition that allows for the study of culture across the animal kingdom (and potentially even beyond, Baluška & Mancuso, 2007). Therefore, we concur that non-human animals possess culture but focus on the specific learning mechanisms that underlie behavioural acquisition in each case. The broadest possible definition of culture – which we adopt here – indeed equates any instance of any variant of social learning with culture itself (Neade, Allritz & Tennie, 2017). According to this minimal definition of culture, a trait is cultural if “social learning of any [variant] plays any role at all in the form and/or the frequency of the behaviour and/or any produced artefacts [...]” (Neade et al., 2017, p. 12). Under this minimal definition, culture is widespread, from insects (e.g. Alem et al., 2016) to apes (e.g. Whiten et al., 2001). Such a broad definition includes the widest range of traits and, perhaps most importantly, circumvents the semantic disputes of the past. Yet, this minimal definition is still fully compatible with questions about the learning mechanisms underlying animal cultures. For example, any culture can be tested for the presence of copying variants of social learning and potential cases of culture-dependent forms. As mentioned above, culture-dependent forms must be based on copying variants of social learning. Therefore, evidence of copying social learning mechanisms in great apes would indicate that these species possess the required learning mechanisms (copying) to transmit (and eventually produce) culture-dependent forms. Consequently, if we could uncover unequivocal evidence supporting the presence of culture-dependent forms in extant apes we could, in turn, indirectly detect their ability for copying.

Evidence of culture-dependent forms in apes would necessarily have to stem from wild or wild-representative captive apes (i.e. those apes living in captivity that are most representative of their wild counterparts). Wild-representative captive apes must be non-enculturated, mother-reared, lacking extensive human training and human interaction and, ideally, living under social conditions which are comparable to wild populations (Henrich & Tennie, 2017). These exclusion criteria are well justified, as extensive human interactions are not available in the apes’ present or past natural environment. Through the process of enculturation (which may involve shaping and moulding the subject’s behaviour either intentionally or unintentionally), apes can acquire abilities and cognitive skills that seem to be beyond the species-typical repertoire of non-enculturated conspecifics (such as action copying; Tomasello et al., 1993; Buttelmann et al., 2007).

In our view, such abilities are not typically ‘awakened’ during the enculturation process but rather installed through training (given the existence of the necessary supporting neural substrates). This is not to say that enculturation is necessarily detrimental for the apes (although see Tennie, 2019b) but rather that it can induce abilities or behaviours not available to wild conspecifics. The possible objection that enhanced abilities present in enculturated ape subjects (such as action copying or communicative abilities based on lexigrams or sign language) could also emerge in special circumstances in the wild is unwarranted: the effects of human enculturation on cognitive abilities do not seem to survive across generations of apes, meaning that even if these abilities were to appear among wild apes, they would likely completely disappear within a generation or two (Tennie, 2019b). However, although cognitive abilities resulting from enculturation do not seem to survive past one generation, certain biological characteristics (such as reproductive rates; Kuze et al., 2012) have been shown to be altered across generations as a consequence of extensive periods of human contact or provisioning in wild-living rehabilitant ape populations.

The presence of culture-dependent forms should also not be assessed in deprived apes, for several reasons. Firstly, it would be unethical to encourage such husbandry practices by conducting research in an institution that deprives apes of social and ecological stimuli. Secondly, impoverished rearing has been shown to cause long-term cognitive deficits in primates (Davenport, Rogers & Rumbaugh, 1973; French & Carp, 2016) rendering experimental results irrelevant. Third, deprived apes are much less likely to show the skills
(and behaviours) of unenculturated and untrained apes. However, we should note that if deprived apes showed evidence of copying and/or culture-dependent forms, this would suggest that the development of these specific skills is somewhat robust against very atypical rearing conditions.

Although the evidence that wild-representative apes can spontaneously copy others is weak, these abilities are commonly assumed in the literature (e.g. Whiten et al., 1999). Previous experiments with great apes have pointed to some copying abilities in the physical domain (emulation learning or copying of environmental results; Hopper et al., 2008). However, these abilities are apparently very limited as they never go beyond what apes can spontaneously re-innovate in the absence of social information (Kohler, 1925; Tennie et al., 2009; see review in Tennie et al., 2020b). Several studies have directly tested whether non-enculturated apes can copy novel behavioural forms that are not present in the species-typical behavioural repertoire by having trained demonstrators perform a novel, rewarded behaviour in front of observer apes. Regardless of behavioural domain, all apes tested so far across three studies failed to copy these novel, unfamiliar behavioural forms (Tomasello, 1999; Tennie, Call & Tomasello, 2012; Clay & Tennie, 2017). In the only experiment to date that tested the ability to copy novel tool-use behaviour in great apes, all four species of apes failed to copy the demonstrated behavioural solution (Tennie et al., 2009). Furthermore, other studies have shown that apes often even fail to apply observed behaviours from within their repertoires to novel situations (Tennie et al., 2012). To our knowledge there exists a single exception of one potentially enculturated ape that might have copied and applied one demonstrated familiar action to a new context (Tennie et al., 2012). Given the data stemming from wild apes regarding peering frequencies of immature individuals (Schuppli et al., 2016), it is worth mentioning that no study to date has investigated the copying abilities of dependent offspring when the mother acts as demonstrator. However, and despite the insights that such experiments could provide regarding mother–offspring social transmission, previous theoretical studies have shown that the conditions under which learning from a single cultural model (for example a single parent) leads to stable cultures are very restricted (Enquist et al., 2010).

Several studies have now shown that wild ape behaviours spontaneously reappear in culturally unconnected populations that have never observed a model demonstrator perform the behavioural form in question (e.g. nettle feeding in gorillas (Tennie et al., 2008); probing in chimpanzees (Lonsdorf et al., 2009); tool-modification to create probing tools in chimpanzees (Hopper et al., 2013); sponging in chimpanzees (Kitahara-Frisch & Norikoshi, 1982); leaf-swallowing in all four great ape species (Huffman & Hirata, 2004; Menzel et al., 2013); food cleaning in gorillas (Neadle et al., 2017); algae scooping and pestle pounding in chimpanzees (Bandini & Tennie, 2017, 2019). Given the results of these studies, it is plausible that ape cultures, as other non-human cultures, consist of culture-independent forms (C. Schuppli, personal communication) that can be acquired without relying on copying and whose re-innovation rate is harmonised and maintained socially via non-copying social learning mechanisms (“socially mediated re-innovations” of so-called latent solutions; Bandini & Tennie, 2017). If this were to be the case, given enough time and motivation, great apes would theoretically be able to learn their behavioural repertoires without copying models. However, this scenario would not exclude a role of non-copying social learning mechanisms. As mentioned above, non-copying social learning mechanisms have a crucial role in determining which and how often variants of behavioural forms that can be learnt individually appear in certain populations. Together with conservatism as a downregulator of further innovations, individual learning and non-copying social learning could create as well as maintain ape cultures.

The evidence outlined above suggests that, as a field, we need to move beyond the assumption that apes systematically rely on copying social learning to acquire novel behavioural forms. Instead, we should first investigate if the products of copying social learning, namely culture-dependent forms, can be found in wild or wild-representative great apes. As we argue below, one approach to this question is to analyse patterns of behavioural variation across populations of great ape species (see also Section VI). However, before we present our method for detecting potential culture-dependent forms in great apes, we will describe previous attempts to analyse cultural patterns in ape species, their main conclusions, and potential limitations. Although these studies did not often directly investigate the underlying mechanisms sustaining these patterns of variation, they often made such inferences. These earlier studies also served as inspiration for the method we develop (the Method of Local Restriction), which specifically targets the evidence for culture-dependency (and consequently copying) in great ape cultures.

III. CHARTING DIFFERENCES IN FORM FREQUENCIES: THE METHOD OF EXCLUSION

(1) Tool use and food processing

The cultural status of great apes (specifically chimpanzees) was originally granted after applying the so-called Method of Exclusion to detect behavioural variation across populations. The general logic of the Method of Exclusion is that, when an effort is made to exclude genetic and ecological factors, behaviours can be classified as cultural (influenced by any variant of social learning) if they are identified in certain populations but absent in others (Whiten et al., 1999). This method was originally used to study wild chimpanzee (Pan troglodytes) behaviour (Whiten et al., 1999, 2001) and was later applied to the other great apes [orangutans, Pongo pygmaeus and Pongo abelii (van Schaik et al., 2003); bonobos, Pan paniscus (Hohmann & Fruth, 2003); gorillas, Gorilla gorilla and Gorilla beringei (Robbins et al., 2016)]. Initially, the Method of
Exclusion mainly focused on tool-use behaviours (technological domain) and food-processing techniques.

The original study (Whiten et al., 1999) collected and compared data on the frequency of 63 potentially cultural behaviours from seven wild chimpanzee sites. The authors concluded that 39 of these behaviours were socially transmitted as they were present at some sites but not at others despite having equivalent ecological settings. However, other factors, such as subtle genetic and/or environmental differences among populations could have also (at least partly) explained the pattern of behavioural variation observed (Laland & Janik, 2006; van Schaik et al., 2009; Koops, McGrew & Matsuzaka, 2013; Koops, Visalberghi & van Schaik, 2014), as the authors themselves recognised to some degree in a later publication (Whiten et al., 2001).

In an attempt to quantify the influence of genetics on chimpanzee behavioural variation, Langergraber et al. (2011) calculated levels of genetic dissimilarity among several chimpanzee communities included in Whiten et al. (1999) and related this measure to the patterns of between-group behavioural diversity described by the study’s authors. Overall, Langergraber et al. (2011) found a significant correlation between genetic and behavioural dissimilarities. However, some behavioural differences were also found between genetically similar groups (but see Lycett, Collard & McGrew, 2007, 2011) making a cultural explanation parsimonious in these cases. In orangutans, Krützen, Willems & McGrew, 2007, 2011) making a cultural explanation parsimonious in these cases. In orangutans, Krützen, Willems & McGrew, 2007, 2011) found that behavioural variation in putative cultural forms could not be explained fully by either genetic or environmental differences among populations. Taken together, these studies illustrate the necessity for considering different potential sources of variation when investigating great ape behavioural diversity and highlight the likely interplay among genetics, environment and learning processes in shaping ape cultures.

Unfortunately, genetics and environmental variation are still being accounted for as sources of variation even in recent studies of ape behavioural diversity across populations. Boesch et al. (2020) recently concluded that copying social learning was the main factor responsible for the differences in hierarchically structured termite-fishing techniques used by chimpanzees in different populations (i.e. programs of termite fishing; Byrne & Russon, 1998). Boesch et al. (2020) based this conclusion on their observation that specific combinations of termite-fishing elements were more similar within communities than among them (although the exact range of overlap in element combinations among communities was not clear). However, the effects that factors such as genetics, environmental differences, social structure and non-copying social learning (see also Bernstein-Kurtycz et al., 2020) play in determining which programs of termite fishing are used in different populations, were not accounted for.

Despite the limitations of the initial study by Whiten et al. (1999), the Method of Exclusion is particularly useful when focusing on differences between neighbouring, genetically interacting (intermixing) communities, as in these cases both environmental and genetic differences can be assumed to be negligible. Examples of traits that differ between neighbouring communities of chimpanzees include the average length of termite- and ant-fishing tools (Koops et al., 2015), the variety of raw materials used to manufacture fishing tools (Pascual-Garrido, 2019), nut cracking efficiency (Luncz et al., 2018), how frequently chimpanzees use stone hammers, and the size of their wooden hammers (Luncz, Mundry & Boesch, 2012; Luncz & Boesch, 2014).

Overall, the general conclusion of Whiten et al. (1999) that culture (at least in a minimal sense) exists in apes is widely accepted. The Method of Exclusion remains a useful first step towards pinpointing cultural candidates, but it alone cannot identify the social learning mechanisms underlying behavioural variation across populations. The Method of Exclusion cannot determine whether a cultural signal is caused by mere differences in behavioural form frequencies (influenced by non-copying variants of social learning and conservatism) or whether it is due to differences in form caused by accumulated deviations during copying events. Therefore, one important aspect that the Method of Exclusion does not address is the question of whether any of these cultural behaviours require copying social learning mechanisms for their acquisition – i.e. whether they are culture-dependent forms. We will return to this question in Section III.4 after presenting a similar approach to the Method of Exclusion in great ape communication.

(2) The gestural domain

Applying the logic of the Method of Exclusion, researchers have also explicitly studied the variation in great ape gestural repertoires across populations within and across species (reviewed by Call & Tomasello, 2007; Byrne et al., 2017). However, in contrast to the original Method of Exclusion (Whiten et al., 1999, 2001), this approach typically included data both from the wild and captivity (see online Supporting Information, Table S1).

Researching gestural communication in chimpanzees, Hobaiter & Byrne (2011b) found that nearly 100% of the gestures they described as present in the wild Sonso chimpanzee community in Uganda had already been reported in earlier studies across a range of wild and captive chimpanzee populations: 100% of the Sonso gestures overlapped with those found at Gombe (wild, Tanzania), 97% with those at Mahale (wild, Tanzania) and 97% with those at Yerkes National Primate Research Center in Atlanta, Georgia (captive, USA). Referring to these findings, Byrne et al. (2017, p. 757) wrote: “[...]: the level of overlap between all chimpanzee studies—captive and wild—was found to be so high that, to a first approximation, the repertoires could be described as the same”. In the case of gorillas, Genty et al. (2009) reported that 85% of the gestures described were found at more than one of the four sites included in the study (three in captivity, and one in the wild), and 39% occurred across all four sites. Cartmill & Byrne (2010) compared the gesture repertoires of captive orangutans across three sites. Out of the 62 gesture...
types that they described, only one gesture was present in just a single population, where it was idiosyncratic to a single individual (Cartmill & Byrne, 2010). Liebal, Pika & Tomasello (2006) compared the gestural repertoires of two further groups of orangutans (both captive). Out of the 30 gestures described, 23 (76%) overlapped between both groups. Knox et al. (2019) compared the repertoires of wild Bornean orangutans (Pongo pygmaeus) and found that, of the 21 gestures described, 20 had been previously reported in captive orangutans. Finally, Pika, Liebal & Tomasello (2005) compared the gestural repertoires of two captive populations of bonobos and found that out of 20 gestures, 18 (90%) overlapped between both groups.

When the repertoires of the three genera of great apes (Gorilla, Pan and Pongo) were compared, they also greatly overlapped (Byrne et al., 2017). Pair-wise repertoire comparisons showed that Pan repertoires overlapped 60 and 80% with those of Gorilla and Pongo, respectively (Hobaiter & Byrne, 2011b). When chimpanzees and bonobo were compared, repertoires overlapped in 88% of their gestures (Graham, Furuichi & Byrne, 2016). Lastly, 89% of the gestures of 1–2-year-old pre-linguistic humans are shared with chimpanzees (Kersken et al., 2019).

Byrne et al. (2017, p. 767) summarised these results as follows: “The great majority of gestures in the ape repertoire […] are innate, in the sense that the potential to develop a particular gestural form and use it for a particular, restricted range of purposes is part of the species’ biological inheritance.” Overall, the findings in ape gestural communication strongly suggest that most gestural forms can independently reappear in – often multiple – culturally unconnected populations of all great ape species (including humans). These results suggest that most ape gestural forms (see Table 1 below for potential exceptions) can be individually re-innovated and are part of the latent behavioural repertoire of great apes. Given the large empirical overlap among ape species, we may even hypothesise that the majority of these gestures were also likely present in a similar form in the gestural repertoire of the last common ancestor of great apes (and perhaps hominin species).

(3) The vocal domain

Great ape vocal repertoires have been studied less often than tool use or gesture repertoires, and studies investigating patterns of vocal variation across populations are rare. Regarding the acoustic structure of great ape vocalisations, these seem to be rather similar across species (and populations) and their forms can be classified broadly into grunts, hoots, screams and barks [Marler (1969) sensu Salmi, Hammerschmidt & Doran-Sheehy (2013)]. Evidence for vocal learning in great apes (and primates) is scarce (Crockford et al., 2004). It is currently widely agreed that the vocal repertoire of great ape species is more or less genetically pre-determined, with some plasticity due to differences in arousal and valence (Fedurek & Slocombe, 2011). In particular, great apes seem largely to be unable to acquire (neither socially nor individually) novel vocal forms that significantly differ from their species-specific repertoire (Janik & Slater, 2000; Fischer, Wheeler & Higham, 2015; but see Lameira, 2017). Nevertheless, claims about the acquisition (or honing) of novel acoustic signals (non-voiced sounds) by captive great apes exist in the literature. “Raspberry” and “extended grunt” in captive chimpanzees (Hopkins, Taglialatela & Leavens, 2007) and “whistling” in a captive orangutan (Wich et al., 2009) have been reported as examples of novel acoustic signal acquisition.

Furthermore, some evidence suggests that great apes can modify (to a certain degree) the acoustic form of vocalisations already within their vocal repertoire. Acoustic modifications (e.g. in mean frequency of the first formant and peak frequency) could have led to the convergence in structure of food grunts after group integration in the study by Watson et al. (2015; but see Fischer et al., 2015). Call structure convergence as a result of call modification was also shown in two male chimpanzee dyads at Mahale (Mitani & Gros-Louis, 1998). There are also reports of significant differences in the structure of pant hoots (e.g. pitch, number of introduction elements, duration of climax scream) between wild neighbouring chimpanzee communities in the Taï forest (Crockford et al., 2004). Overall, there is evidence that apes present some degree of (perhaps socially mediated) plasticity in the production of vocalisations (e.g. changes in the mean acoustic frequencies of calls), but so far, there is no evidence that they can copy new vocal forms (Fischer & Hammerschmidt, 2019).

Similar to the efforts made for charting geographical variation in other behavioural domains explored above, several studies have attempted to map patterns of presence and absence of great ape vocalisations across populations. de Waal (1988) compiled the vocal repertoire of captive bonobos from one institution and compared it with wild chimpanzee vocalisations, identifying 12 vocalisation types in bonobos, all of which had a comparable correlate in wild chimpanzees. Similarly, Hardus et al. (2009) compared orangutan calls across seven wild populations, one captive population and one population of rehabilitant orangutans. Out of the 32 calls that they identified, 25 appeared in more than one orangutan population. Yet, it is important to note that several of these calls were actually differentiated not based on their acoustic structure (their form), but on the context of use. One of the calls that was present in only one population appeared in other contexts in other populations in seemingly in the same form (“squeak”/“fear squeak”), and two calls were performed exclusively and idiosyncratically by a single individual in captivity (“whine” and “fear whine”). Wich et al. (2012) compared nesting calls and mother–infant calls in five wild orangutan populations, and also calculated the genetic distances between the populations studied. The authors found that nest- and mother–infant calls were present in some populations but absent in others and that call form in these two contexts also differed between some of the populations. Three of the calls (“nest smack”, “harmonic uuh”, and “throat scrape”) were considered group specific
cases of cultural variation, whilst the fourth (“raspberries”) was found in more than one population. Based on their results, Wich et al. (2012, p. 7) suggested “[...] that these sounds were invented in each population and subsequently spread through social learning [...]”. Salmi et al. (2013) compiled the vocal repertoire of two groups of western lowland gorillas and described 17 different vocalisations. When compared with the vocal repertoire of mountain gorillas, 16 of the 17 vocalisations were found to overlap between these two species. “Sex-whinny”, which was found in western – but not mountain – gorillas seemed to be a context-specific version of “whinny”, which was found in both species (Salmi et al., 2013). In summary, the few studies that have applied the Method of Exclusion to great ape vocalisations show that there exist certain differences among populations and thus apes possess vocal cultures in a minimal sense. However, vocal forms are not necessarily copied from other individuals as they appear in culturally unconnected populations. Non-copying variants of social learning seem to play a role shaping vocal repertoires given the evidence that vocalisations can be modified in response to external stimuli (reviewed by Fischer & Hammerschmidt, 2019).

(4) Why a new method (the Method of Local Restriction) is required

The Method of Exclusion remains a useful tool to identify cases of cultural variation via differences in form frequencies across populations. However, the Method of Exclusion does not allow assessing if copying likely plays (or played) a role in establishing those cultures. In order to evaluate the potential role of copying in great ape cultures it is necessary to investigate the specific patterns of form distribution across populations.

Whenever independent re-innovations of behavioural forms occur (or can be inferred) in different, culturally unconnected populations, the most parsimonious explanation should be that the behavioural form is not transmitted via copying. Instead, forms that appear in unconnected populations would represent latent solutions (Tennie et al., 2009). Latent solutions are defined as culture-independent forms that can be individually re-innovated without the need for copying a model and that are mediated by non-copying social learning mechanisms (Tennie et al., 2009). To avoid a priori assumptions about a role of copying social learning in behavioural acquisition, the null hypothesis for great ape cultures should be that all wild ape behavioural forms represent latent solutions (especially considering the above-mentioned studies showing that apes do not spontaneously copy novel forms).

Conversely, in our search for the most likely cases of form copying in great apes, we are interested in behavioural forms that have not been re-innovated elsewhere. The process of identification of these forms is what we call the Method of Local Restriction: a search of forms that do not appear outside culturally connected populations and that constitute candidate culture-dependent forms. In this way, the Method of Local Restriction provides information regarding the likelihood that copying underlies the acquisition of an ape behavioural form. Thus, it is important to consider that the Method of Local Restriction only allows drawing indirect inferences about copying and does not provide direct evidence of a role of copying in behavioural acquisition. Instead, the Method of Local Restriction allows us to pinpoint the most likely cases of culture-dependent forms which can be investigated in follow-up studies (see Section VI).

Introducing and following this general line of logic, Byrne (2007) re-evaluated the list of cultural behaviours compiled using the Method of Exclusion in chimpanzees (Whiten et al., 2001), focusing on the extensive overlap in behavioural forms across sites. Byrne (2007, p. 579) concluded that most behavioural forms are “not difficult for chimpanzees to invent, and that invention has occurred independently at many sites”. These independent occurrences referred to by Byrne (2007) represent cases of repeated, individual re-innovations of the behavioural forms in each of the populations studied (likely mediated by non-copying social learning mechanisms). Instead of focusing on behavioural overlap, in the following sections we take the complementary approach of using the Method of Local Restriction to search all behavioural domains in all species of great apes for behavioural forms that are not shared across culturally unconnected populations.

IV. Locally Restricted Forms Remain Undetected by the Method of Exclusion

Identifying a behavioural form whose acquisition depends causally on copying social learning mechanisms would suggest that the form in question is culture-dependent in the respective great ape species. The existence of at least one such form would in turn indicate that non-human great apes possess certain cognitive abilities deemed crucial for the development and sustenance of cumulative culture in modern humans (a conclusion that could then be tentatively extrapolated to the last common ancestor of that great ape species and hominins; Tennie et al., 2017). Instead of merely focusing on the overlap between behavioural repertoires from different populations (as the Method of Exclusion does), we took the complementary approach of the Method of Local Restriction. Our method focuses on those forms that do not repeat in culturally unconnected populations, as these are the best candidates for culture-dependent forms given the lack of independent, individual re-innovation elsewhere. We labelled these forms locally restricted forms. As mentioned before, if copying underlies trait acquisition, copying error would have led to forms that are path-dependent and population specific. Consequently, finding locally restricted forms in apes would provide indirect evidence for copying in the ape species in question. These forms could then be tested...
for their dependency on copying in follow-up experiments (see Section VI).

In our application of the Method of Local Restriction, we defined locally restricted forms as those expressed by at least two individuals of a single population or population cluster of one species that do not occur in another unconnected population (Fig. 1). Locally restricted forms must have been observed in at least two individuals in order to exclude idiosyncratic behaviours (Tomasello et al., 1994; Call & Tomasello, 2007). Locally restricted forms do not need necessarily to be restricted to a particular species. That is, locally restricted forms of species A also can be present in additional populations of species B, but they can only appear in one population (or population cluster) of species A if they are to count as locally restricted in that species (i.e. in species A).

We differentiate an important subtype of locally restricted forms that we named locally unique. Locally unique forms are locally restricted forms as defined above but with the additional characteristic that they are not found in any other (unconnected) population of any other ape species. Unlike other locally restricted forms, locally unique forms are and must be exclusively present in one population (or population cluster) of only one great ape species (Fig. 1). Locally restricted forms – and especially locally unique forms – represent the most likely cases of culture-dependent forms and copying in apes (although, in and of themselves, they cannot prove either and require further examination; see Section VI).

In the following section we present the methods and results of the application of the Method of Local Restriction to great apes. We applied this method across all species of apes, all populations and all behavioural domains for which there were enough data (tool use, food processing, gestures and vocalisations/sounds, although note that we did not exclude any behavioural form from any domain).

V. APPLYING THE METHOD OF LOCAL RESTRICTION: IN SEARCH OF POTENTIAL GREAT APE CULTURE-DEPENDENT FORMS

In order to determine which behavioural forms are locally restricted, we first analysed published behavioural repertoires across behavioural domains of wild and captive chimpanzees (Liebal, Call & Tomasello, 2004; Call & Tomasello, 2007; Hobaiter & Byrne, 2011b; Boesch et al., 2020; Tomasello et al., 1985, 1994, 1997; Tomasello, Gust & Frost, 1989; Whiten et al., 1999, 2001; behavioural categories 6, 7 and 8 from Nishida et al., 2010; Roberts, Roberts & Vick, 2014), bonobos (de Waal, 1988; Hohmann & Fruth, 2003; Pika et al., 2005; Graham et al., 2016), gorillas (Pika, Liebal & Tomasello, 2003; Pika, 2007; Genty et al., 2009; Salmi et al., 2013; Robbins et al., 2016) and orangutans (Liebal et al., 2006; Hardus et al., 2009; van Schaik et al., 2009; Cartmill & Byrne, 2010; Wich et al., 2012). To identify potential locally restricted behaviours, we followed the steps listed below.

(1) From the studies cited above, we selected those behaviours that were present in a single population or population cluster and whose form was unlikely to be the product of environmental factors (according to the authors). We did not include forms that were present at more than one site, if the sites were not connected by migrating individuals as reported in the literature (or visual contact in captive settings). If no migration data between sites were available, we considered as unconnected populations those that were more than 50 km apart (Herbinger, Boesch & Rothe, 2001) or separated by geographic barriers such as rivers more than 8 m wide (Bender & Bender, 2013). If the study only included one population, we considered all described behaviours as possibly restricted to that population unless we could confirm that the behavioural form was present elsewhere.

(2) We conducted an additional literature search on Google Scholar for reports of potential locally restricted behaviours that were not included in the studies cited above. To conduct this new search (carried out by A.M.-R. between March 2018 and November 2020), we used the terms ‘restricted behaviour’, ‘new behaviour’, ‘local behaviour’, ‘local tradition’, and ‘new tradition’ in combination with specific great ape species names and the terms ‘population’ and ‘group’. As before, we only included behavioural forms that had been originally observed in at least two individuals to avoid selecting idiosyncratic behaviours. However, it was not
always possible to determine the number of individuals that performed the behavioural form. In such cases, we still included the behaviour in our list but labelled it accordingly (number of individuals observed: ‘unknown’).

(3) We conducted an additional search for reports of potential candidate locally restricted forms using the published names of the behaviours obtained from the two previous steps. In particular, we searched for reports of these behavioural forms in additional, culturally unconnected populations from those where the behaviour was reported as restricted. In addition, we looked for these behaviours in the same and other great ape species.

(4) We invited ape experts to contribute to the creation of our list by adding new locally restricted behaviours that we had not found in our literature search, and/or by providing data on additional populations (of any great ape species) where our candidate locally restricted forms had been observed. These collaborations are indicated as personal communications in Table S2 (although we also offered anonymised contributions).

(5) Additionally, we created a collaborative webpage (https://sites.google.com/view/group-specific-ape-behaviors/home) including our current list of locally restricted and unique behaviours (Table 1). The main reason for the creation of this online resource is that identifying locally restricted behaviours is necessarily an ongoing project that should be updated with future observations on The Method of Local Restriction website. Moreover, it was not feasible personally to contact all known great ape researchers individually in Step 4. This website provides an online platform to establish a large-scale and enduring collaboration to help identify both new locally restricted behaviours or new populations where locally restricted behaviours have been observed. Scientists, vets, ape keepers, field researchers and other ape experts are invited to visit the webpage and contact the authors regarding additional observations.

(1) Results of the Method of Local Restriction
The initial list of reports of locally restricted behaviours derived from Steps 1 and 2 above included 126 entries across all four great ape species based on the authors’ classification (see Supplementary Table S2). Following our search in the published literature for additional unconnected populations where these reported locally restricted behaviours were present (Step 3) and after consulting with great ape experts (Step 4), this list was reduced to 25 behaviours at the time of submission (Table 1). Of these 25 locally restricted forms, three were locally unique forms (Table 2) – i.e. forms that are currently only known from a single population, or population cluster, of a single ape species. The remaining 22 forms were

Table 1. Locally restricted (and locally unique) behaviours in great apes by behavioural domain

| Species | Food use | Environment-related | Gestures | Vocalisations/calls |
|---------|---------|---------------------|----------|-------------------|
| Chimpanzees (Pan troglodytes) | 3 (‘branch-beak’, ‘branch-beak’, ‘branch-beak’) | 0 | 0 | 0 |
| Orangutans (Pongo abelii and Pongo pygmaeus) | 2 (‘ape cop’, ‘ape cop’) | 0 | 0 | 0 |
| Gorillas (Gorilla gorilla and Gorilla beringei) | 3 (‘tongue out’, ‘tongue out’, ‘tongue out’) | 0 | 0 | 0 |
| Bonobos (Pan paniscus) | 2 (‘tongue out’, ‘tongue out’) | 0 | 0 | 0 |
found in additional populations of different great ape species from those where they were originally described as restricted (Table 3).

Initially, we only considered behavioural forms from four domains: tool use, food processing, gestures and vocalisations/sounds. However, we found that some locally restricted behaviours could not be adequately classified within these categories. Following Robbins et al. (2016) we classified as environment-related those behaviours that involved a physical component of the environment and not another individual, but were not related to foraging. In addition, when we compiled our list, there were some behaviours that we could not easily classify within any defined domain, since the goal/context of the behaviours was not clear from their descriptions. However, as we were interested in locally restricted forms regardless of domain, we did not exclude them.

We found an extensive overlap of behavioural forms across great ape species (and occasionally other primates) and domains (Table S2). This overlap suggests that different ape species share, to a large degree, a common behavioural repertoire of latent forms.

In the tool use domain, our results suggest that given similar or equivalent environmental conditions, all great apes seem to use tools in a comparable way. Indeed, we did not find any locally unique tool behaviour in any great ape species. We identified several locally restricted tool behaviours, which were locally restricted in one species but were also found in other primate species (Tables 1 and 3). It may not be surprising that gorillas originally showed the lowest number of tool behaviours, as gorilla tool use frequency in the wild is known to be low compared to the other two non-human great ape genera, *Pongo* and *Pan* (Breuer, Ndoundou-Hockemba & Fishlock, 2005). However, the fact that we could not find any locally unique (nor locally restricted) tool behaviour in orangutans, who are proficient tool users in the wild, suggests that our method compensates for differences in natural frequencies of tool use among species. We only found one food-processing behaviour that was locally unique (“fruit detachment with feet” in bonobos) and one that was locally restricted (“dug hole drinking” in gorillas).

In the gestural domain, we did not find any locally unique gestures in any great ape species. Locally restricted gestures were found in all ape species except gorillas. Numerically, bonobos had the highest number of locally restricted gestures compared to the other species (Table 1). Variation in the number of locally restricted behaviours (including gestures) reflects, most likely, differences among great ape species in the number of populations studied and the duration of these studies. Chimpanzees were the first species for which a gestural repertoire was compiled in the wild (Hobaiter & Byrne, 2011b), and more studies in captivity have been dedicated to the study of chimpanzee gestures than to any other ape species. Consequently, chimpanzee gestures are available from a wider sample of populations, which allows for a broader and more exhaustive comparison. The relatively small number of gestural repertoires recorded from other populations of great ape species could have affected our list in two ways: firstly, it could have led to an underestimation of locally restricted gestures because these have not yet been described, or, secondly, to an overestimation of locally restricted gestures due to a lack of comparative data from additional populations. With more gestural data being published, we will hopefully be able to adjust our conclusions (please use The Method of Local Restriction website https://sites.google.com/view/group-specific-ape-behaviors/home to report further occurrences).

In the vocalisation/sound domain, one locally unique vocalisation and one locally restricted sound were found among Sumatran orangutans (*Pongo abelii*; “harmonic uuh” and “grinding”). The “harmonic uuh” is a call performed by all mothers in the Ketambe population (Sumatra) to call their infants just before retrieving them. “Grinding” was found in rehabilitant orangutans (Rijksen, 1978) and was interpreted as a fear sign when individuals finished quarantine and were reintroduced to a group. Subjects recently caught from the wild also usually performed this behaviour. Grinding is also present in Bornean orangutan infants at Twycross zoo (UK) who perform this behaviour when displaying towards keepers. No further locally unique or locally restricted vocalisations/sounds were found in any great ape species.

In the environment-related category, we found one locally restricted form in bonobos (“branch slap”). It is possible that this locally unique/restricted form that we found in the environment-related domain is related to particularly unique environmental conditions occurring in that population. The lack of additional bonobo populations where “branch slap” occurs could be the result of the few bonobo behavioural repertoires published. Given that other unconnected great ape populations of two species also perform this behaviour (Table S2), it seems plausible that when more data are available, this behaviour will be reported from other unconnected bonobo populations.

We found one locally unique form (“tooth brushing”) and one locally restricted form (“mouth washing”) in gorillas that we classified as belonging to our ‘other’ domain; these behavioural forms could potentially be hygiene-related.

VI. ARE LOCALLY RESTRICTED BEHAVIOURS CULTURE-DEPENDENT FORMS?

The Method of Local Restriction allows us to identify potential culture-dependent traits in animals based on the premise that behaviours only found in one population of a single species may be less likely to be re-innovated elsewhere via socially mediated individual learning. These forms could therefore be dependent on copying social learning to be locally acquired.

Although we believe that the Method of Local Restriction provides a useful [and necessary] first step towards identifying culture-dependent traits in great apes, copying social
learning cannot be unambiguously identified even using this method. For example, locally unique forms could be the result of (sometimes subtle) local environmental factors. In such cases, individuals expressing these forms would not necessarily have acquired them via copying but rather via individual learning mediated by non-copying social learning mechanisms. As a hypothetical example, gorillas in Bai Hokou might include in their diet a locally available, very sticky plant that leaves a gummy substance in the teeth after being consumed. The consumption of such a plant could then lead the gorillas in this population to rub their teeth with their finger in order to remove the uncomfortable sticky substance. In addition, genetic predispositions might influence the behavioural repertoires of ape populations. As another hypothetical example, chimpanzees at Sonso could have a genetic condition that makes their skin particularly dry. This condition could cause the chimpanzees extreme itchiness (particularly on their backs) which they relieve by using lianas. The above-mentioned hypothetical examples illustrate the fact that although local restriction, and especially local uniqueness, are compatible with a scenario in which copying social learning underlies behavioural form acquisition, other explanations are possible. That is, even the Method of Local Restriction can result in false-positive cases of copying.

In order to conclude robustly that copying is ultimately responsible for local restriction, additional evidence is needed. Such evidence can be obtained by testing whether locally restricted and unique behaviours are re-innovated during baseline tests (Bandini & Tennie, 2017, 2019, 2020; Bandini et al., 2020). During baseline tests, individuals naïve to the target behaviour are provided with the raw materials necessary to perform the behaviour in question. If, in the absence of a model, naïve subjects perform the behavioural form, this logically shows that copying social learning is not required for the acquisition of the behavioural form (Bandini et al., 2020). Thus, any form appearing in a baseline test cannot be a culture-dependent form (by definition). However, negative data from baseline tests are also informative, as they are indirect evidence that the target behaviour may require copying (Bandini et al., 2020). Yet, clear evidence for supporting a culture-dependence argument would require not only that the target behaviour resists spontaneous re-innovation in a baseline test, but also that the target behaviour appears once demonstrators have modelled the behaviour to observers (Bandini & Tennie, 2018; Bandini et al., 2020; Neadle, Bandini & Tennie, 2020). That is, the target form must fully resist individual re-innovation and must be expressed after observing it.

In future, baseline tests should be undertaken for the 22 locally restricted and three locally unique behavioural forms that we identified using the Method of Local Restriction (Tables 1 and S2). We urge researchers to join our efforts to systematically test the contributions of individual and social learning mechanisms to the acquisition of these forms following the test protocol outlined in Bandini et al. (2020).

A more direct way to rule out culture dependence (and with it, copying social learning) in locally restricted behaviours would be to observe these forms in additional, culturally unconnected populations (both in the wild or in captivity). These observations would, in essence, represent outcomes of natural baseline tests. And so, we again urge readers to contribute to these efforts by sharing with us observations of any locally restricted or locally unique forms as described above on the Method of Local Restriction website (https://sites.google.com/view/group-specific-ape-behaviors/home).

### VII. DISCUSSION

We described and applied a novel methodology, the Method of Local Restriction, to compile the most likely cases supporting the existence of copying social learning (and culture-dependent forms) in non-human great apes across all behavioural domains. Focusing on behavioural forms restricted or unique to certain populations and despite certain limitations (which we discuss below), our methodology represents an important step in assessing which learning mechanisms likely underlie the maintenance of great ape behavioural repertoires. The results we obtained using the
Method of Local Restriction show that the vast majority of great ape behavioural forms across all ape species, populations and behavioural domains (tool use, food processing, gestures, vocalisations/sounds and environment-related behaviours) are most likely not culture-dependent forms, but rather culture-independent latent solutions (as they appear in similar form in culturally unconnected populations). These latter forms are most likely socially mediated individual re-innovations (Bandini & Tennie, 2017), that appear often to be shared (to a large degree) among ape species.

To date, the most complete behavioural repertoire of any great ape species has been compiled for chimpanzees (Nishida et al., 2010), and it includes 891 behavioural forms. If we take this value as even a minimal approximation of the great ape behavioural repertoire size, we find that much less than 1% of behaviours (N = 3) are locally unique. However, this value is just an estimate, as the total number of great ape species is not known.

Table 3. Candidate locally restricted behaviours in great apes. The names of the behaviours are those used in the original references. The definitions have been modified for the sake of simplicity and to highlight underlying forms. Original definitions can be found in Table S2.

| Behaviour          | Definition                                                                 | Species | Original reference               | Original population       |
|--------------------|-----------------------------------------------------------------------------|---------|----------------------------------|---------------------------|
| Branch-hook        | Branch used to hook other branch                                            | Chimp   | Whiten et al. (2001)             | Bosou (Guinea)            |
| Liana scratch      | Grasp a flexible, long object that is attached on both ends, pulling it down-  | Chimp   | Hobaiter & Byrne (2010)          | Sonso (Uganda)            |
|                    | wards or sideways in order to hold it taut, and then rub body against it     |         |                                 |                           |
| Nasal probe        | Clear nasal passage with a stick                                             | Chimp   | Whiten et al. (2001)             | Mahale M (Tanzania)       |
| Nipple stimulate   | Press digit tip(s) against own nipple(s)                                     | Chimp   | McGrew & Marchant (2001)         | Mahale M (Tanzania)       |
| Rub                | Hand makes back-and-forth movement on another’s body without losing contact | Chimp   | Roberts et al. (2014)            | Sonso (Uganda)            |
| Tandem walk        | Place arm over the body of the recipient and then both walk forward (while  | B Orang | Cartmill & Byrne (2010)          | Twycross Zoo (UK)         |
|                    | maintaining position)                                                        |         |                                 |                           |
| Tongue out         | Protrude tongue                                                              | B Orang | Cartmill & Byrne (2010)          | Twycross Zoo (UK)         |
| Grinding           | Audible grinding of the teeth                                                | S Orang | Hardus et al. (2009)             | Ketambe rehabilitans in Sumatra |
| Dug hole drinking  | Dig a hole on edge of water, wait for hole to fill with water and then drink it | W Gor   | Robbins et al. (2016)            | Bai Hokou (Central African Republic) |
| Lap cover          | Cover lap with objects (e.g. vegetation) during resting                     | M Gor   | Robbins et al. (2016)            | Karisoke (Rwanda)         |
| Mouth washing      | Take water into mouth, then move it back and forth within mouth before swall-  | W Gor   | Robbins et al. (2016)            | Bai Hokou (Central African Republic) |
|                    | ow ing                                                                            |         |                                 |                           |
| Shaking leaves     | Shake objects (e.g. tree leaves) to clean off dirt                           | W Gor   | Robbins et al. (2016)            | Moukabala (Gabon)         |
| Branch slap        | Slap noisily on either a branch or a tree’s trunk                           | Bon     | Hohmann & Fruth (2003)           | Lomakala (DCR)            |
| Chest beat         | Slap repetitively on own chest with alternating open hands or knuckles      | Bon     | de Waal (1988)                   | San Diego Zoo (USA)       |
|                    |                                                                                       |         | in Pika et al. (2005)            |                           |
| Fly whisk          | Use small, long objects (e.g. leafy twigs) to shoo away sweat bees (e.g. from  | Bon     | Hohmann & Fruth (2003)           | Lomakala (DCR)            |
|                    | genital swellings)                                                             |         |                                 |                           |
| Groom slap         | Flat palm strike by a groomer on a groomee                                   | Bon     | Hohmann & Fruth (2003)           | Lomakala (DCR)            |
| Leaf clip          | Ripping of leaves from ground vegetation or from trees                        | Bon     | Hohmann & Fruth (2003)           | Lomakala (DCR)            |
| Leaf sponge        | Use of a sponge made of chewed leaves to dip water from tree hole             | Bon     | Hohmann & Fruth (2003)           | Lomakala (DCR)            |
| Lower head         | Grooming partner flexes the neck to offer the top of head for grooming        | Bon     | Nishida et al. (1999)            | Wamba (DCR)?              |
|                    |                                                                                       |         | in Pika et al. (2005)            |                           |
| Move hand and      | Move hand and arm across (presumably own) body                                | Bon     | Savage & Bakeman (1978)          | Yerkes Primate Center (USA) |
| arm across body    |                                                                                       |         | in Pika et al. (2005)            |                           |
| Teeth chatter      | Rapidly chatter together the upper and lower teeth rows                       | Bon     | Hohmann & Fruth (2003)           | Lomakala (DCR)            |
| Vegetation seat    | Bend small trees or shrubs to the ground and sit down on the leafy parts      | Bon     | Hohmann & Fruth (2003)           | Lomakala (DCR)            |

Chimp, chimpanzee; B Orang, Bornean orangutan (Pongo pygmaeus); S Orang, Sumatran orangutan (Pongo abelii); W Gor, western lowland gorilla (Gorilla gorilla gorilla); M Gor, mountain gorilla (Gorilla beringei beringei); Bon, bonobo (Pan paniscus).
ape behavioural forms has not yet been calculated (although we would expect it to be around 5000; a much lower number of behavioural forms than in humans). Regardless of the actual number of great ape behavioural forms, our results show that locally unique forms (which represent the most likely candidate culture-dependent forms), constitute a very small fraction of great ape repertoires.

According to our results, the vast majority of ape behavioural forms can best be explained as follows: individual learning underlies the acquisitions of these forms, while non-copying social learning influences – and even stabilises – the selection and frequency of the forms in the affected populations (Tennie et al., 2009; Bandini & Tennie, 2019) with conservatism restraining the number of expressed latent solutions (see also Hrubesch et al., 2009). The existence of such latent solutions is not only the most parsimonious hypothesis to date for ape behavioural repertoires, as it does not assume the need for copying variants of social learning, but also the largest encompassing hypothesis for great ape culture and behaviour. This scenario is also in agreement with the outcome of natural experiments (inferable and observed independent re-innovation across populations and ape species) and with baseline tests where, in the majority of cases, the target forms were re-innovated by naive individuals after observing models performing these behaviours in the literature – e.g. due to unpublished results or the amount of data to be analysed. It was precisely for these two reasons that we consulted with experts in the field of great ape behaviour (Step 4) prior to the completion of this manuscript. These were also the reasons why we created an online resource, The Method of Local Restriction website, for researchers to continuously update the locations where the listed behaviours have been observed, as well as adding additional candidate locally restricted behaviours. As more observations are added to this website, and more repertoires are published from across different locations, we will be able to refine which behaviours are truly locally restricted. Large-scale projects, such as the ongoing Pan African Project: the Cultured Chimpanzee (PanAF), will be of particular help revealing the full scope of the overlap and specificity of behavioural forms across wild great ape populations. Consequently, we welcome compilations of great ape behavioural data in publications such as Boesch et al. (2020), even though we at times disagree with their interpretation.

Third, the initial numbers of behaviours that we compiled for each species could have been influenced by discrepancies in research intensity. Differences in the number of populations studied and general observation time per species could have influenced the initial amount of locally restricted candidates we compiled. Chimpanzees, for instance, have been systematically studied for a longer time than all the other great ape species (Lampanathan, 2011). However, following our Method of Local Restriction, understudied

(1) Limitations in data input

First, we encountered the difficulty that authors often use different terminology to describe the same behavioural form. When enough details were provided, we could circumvent this problem by comparing the descriptions of the behaviours directly, but this was sometimes not possible. Moreover, great ape experts also helpfully provided additional examples of equivalent behaviours named differently in the literature. Projects such as the Great Ape Dictionary are a valuable resource for comparative research as they provide graphical examples of great ape gestures. The ethogram of the Mahale chimpanzees compiled by Nishida et al. (2010) was also a useful resource for determining and comparing behavioural forms. It would be a welcome development if more sites and research groups would create behavioural libraries – including video footage – from different behavioural domains, species, and sites. These archives would also allow us to conduct reliability analysis to ensure that behaviours named similarly or described in a similar way in the literature are indeed the same behavioural forms. Regarding vocalisations we also encountered the problem that we had to rely on nomenclature to compare vocal repertoires between populations, as comparison of more precise acoustic structures often was not available. Ultimately, an attempt to produce complete ethograms – at least regarding underlying forms – for all ape species across all domains (with audio, photographic and video examples) would be a worthwhile, if daunting, project.

Second, given the difficulties described above, it is certainly possible that we overlooked further potential locally restricted behaviours, as well as additional descriptions of behaviours in the literature – e.g. due to unpublished results and the amount of data to be analysed. It was precisely for these two reasons that we consulted with experts in the field of great ape behaviour (Step 4) prior to the completion of this manuscript. These were also the reasons why we created an online resource, The Method of Local Restriction website, for researchers to continuously update the locations where the listed behaviours have been observed, as well as adding additional candidate locally restricted behaviours. As more observations are added to this website, and more repertoires are published from across different locations, we will be able to refine which behaviours are truly locally restricted. Large-scale projects, such as the ongoing Pan African Project: the Cultured Chimpanzee (PanAF), will be of particular help revealing the full scope of the overlap and specificity of behavioural forms across wild great ape populations. Consequently, we welcome compilations of great ape behavioural data in publications such as Boesch et al. (2020), even though we at times disagree with their interpretation.

Third, the initial numbers of behaviours that we compiled for each species could have been influenced by discrepancies in research intensity. Differences in the number of populations studied and general observation time per species could have influenced the initial amount of locally restricted candidates we compiled. Chimpanzees, for instance, have been systematically studied for a longer time than all the other great ape species (Lampanathan, 2011). However, following our Method of Local Restriction, understudied
species or domains would be more likely to exhibit a greater number of locally restricted behaviours than species studied more intensively, as fewer comparative data from additional populations are available (see examples from bonobos in Section V.1).

Fourth, differences in population size are likely to cause differences in innovation rates (Shennan, 2001; Kline & Boyd, 2010), and different innovation rates will influence the number of locally restricted behaviours in a population, regardless of whether copying social learning is present/required or not. Smaller populations are more likely to have smaller behavioural repertoires because innovations are less likely to occur with smaller population sizes. On the other hand, larger, more gregarious populations present more possibilities for various forms of social learning because more between-individual encounters take place (Whiten & van Schaik, 2007). Given that wild apes are declining in numbers, and that reducing population sizes can reduce repertoire size (Kühl et al., 2019) we may be losing the opportunity to compile a fully comprehensive list of behaviours present across ape populations over time.

(2) Limitations in data analysis

In our method, data analysis was limited by the fact that different projects have often used slightly different reference repertoires when coding behaviours – especially gestures – depending on the level of detail included in the gesture category (Pika & Fröhlich, 2019). We could correct for some of these instances when consulting with experts on primate gestural communication, who informed us about changes in the degree of grouping of gestural forms since the publication of their papers. Nevertheless, it is possible that we did not account for all these instances. In addition, gestural forms are currently classified according to the meanings assigned by the human observers rather than by the species in question (Hobaiter & Byrne, 2014; Graham et al., 2018). Consequently, it is possible that the descriptions of the gestural repertoires of great apes will change in future based on a shift in focus from the ape gesture meanings attributed by humans to the gesture meanings understood by apes.

Furthermore, it was not always possible to search effectively for certain candidate locally restricted behaviours in additional publications due to the somewhat ambiguous descriptions given for certain behaviours. As an example, one of the candidate locally restricted behaviours was defined as “move hand and arm across body” [Savage & Bakeman (1978) sensu Pika et al. (2005)]. This definition is ambiguous since the action described could be part of several gestural forms, such as “loud scratching” or “wiping hair”. The lack of detail in this definition makes it impossible to compare with the published repertoires. If more precise definitions were made available, we suspect that this behaviour would be found in additional populations, lowering the number of locally restricted behaviours. The Method of Local Restriction website will allow for constant revisions of descriptions of behaviours, which will ameliorate some of the limitations we encountered during data analysis.

(3) Limitations in data output

First, it remains to be determined if locally restricted behaviours (especially locally unique behaviours) can be individually re-innovated by naïve individuals when suitable environmental conditions exist. Future studies should investigate if the locally restricted behaviours that we found can be elicited when following the extended latent solutions methodology (Bandini & Tennie, 2018; see also Section VI).

Second, we cannot rule out the possibility that we underestimated the number of locally restricted behaviours due to potential false negatives in our sample. Five of the 126 candidate locally restricted behaviours that we initially identified in the literature were found in additional populations of rehabilitant orangutans (and thus not considered locally unique). These rehabilitant individuals were reintroduced to forests different from their native ones, which did not have a local population that provided social learning opportunities of any kind (Russon et al., 2009). Consequently, these rehabilitant populations are culturally unconnected from wild populations and presented a large-scale latent solution test to assess socially mediated individual learning of wild orangutan behaviours. However, it was not possible to determine the degree of human enculturation these individuals might have experienced since they were captured during infancy and were exposed to human contact in the rehabilitation centres (Russon et al., 2009). In our review, we assumed that these individuals were not enculturated as no specific training was described in Russon et al. (2009). If we underestimated the level of enculturation of these individuals and they were, in fact, enculturated, this population of rehabilitant orangutans would not be wild-representative, and thus would have to be excluded from our literature search. If that is the case, the additional observations in these rehabilitant orangutan populations that were used to rule out potential locally restricted behaviours ought to be excluded, increasing the number of locally restricted behaviours in orangutans.

Third, there remains the theoretical possibility that forms present across culturally unconnected populations are sometimes sustained via copying. In this case, our method would not have detected local restriction and consequently would have missed such behaviours. Although our method does not automatically rule out the possibility that behavioural forms present in the same form in unconnected populations are acquired via copying, this theoretical possibility is unlikely for several reasons.

First, previous studies have shown that apes do not spontaneously copy what they can not already do on their own [e.g., see Clay & Tennie (2017) and references therein] and many wild ape behaviours have already been shown not to depend on copying (as they are re-innovated by form-naïve individuals; see Section II). Alternatively, local genetic predispositions and/or environmental channelling (and other factors, such as dominance styles) could also catalyse similar
forms across different populations (Galef, 1992; Tomasello, 1999). But note that in these latter cases, copying would not actually need to contribute to the acquisition and maintenance of the form in the population.

Second, as we argued above, the repeated transmission of behavioural forms between individuals via copying leads to unavoidable copying error that should result in path-dependent behavioural forms over time (i.e. differences among populations). A possible exception is that when behavioural forms have been recently innovated, copying error might not yet have caused divergent cumulation of modifications. Thus, our method would be less effective in detecting newly innovated culture-dependent forms than older ones. However, as time goes by, path-dependent modifications due to copying error would cumulate in newly innovated behaviours and eventually we would be able to detect locally unique forms in these populations even if these are currently undetectable.

(4) The role of social learning in behavioural form acquisition

According to our results, the vast majority of ape behavioural forms [including those behaviours proposed as examples of cumulative culture in great apes (e.g. Boesch 2003), see Section I] are not locally restricted and therefore their acquisition is more likely mediated by an interaction of individual learning, non-copying social learning mechanisms and conservatism rather than by copying social learning. Neither our paradigm nor our results, however, deny the possibility that social learning processes influence the frequency of these individual re-innovations at different ontogenetic stages (see also Schuppli & van Schaik, 2019). On the contrary, data conclusively show that non-copying social learning mechanisms increase and maintain the frequency of behavioural forms within a culturally connected group, producing the observed wild great ape cultural patterns (e.g. Tennie et al., 2008, 2009; Allritz, Tennie & Call, 2013; Menzel et al., 2013; Reindl et al., 2016; Bandini & Tennie, 2017, 2019; Neadle et al., 2017). These differences in frequencies can be detected by the Method of Exclusion mentioned above, as they can lead to the differential accumulation of behavioural forms between populations (see also Schuppli & van Schaik, 2019).

Several authors and working groups have also been very prolific in the debate on the learning mechanisms behind gestural acquisition and usage. Some of this work has focused on describing potential social learning mechanisms that shape gestural repertoires, influencing gesture frequency and use. Hobaiter & Byrne (2011a) suggested that juvenile chimpanzees produce gestures in rapid sequences because they are unsure of which is the appropriate – or most effective – gesture for achieving a particular outcome. This early phase would be equivalent to the trial-and-error phase described for nut cracking (Inoue-Nakamura & Matsuzawa, 1997). As they grow, chimpanzees only use the most effective gestures from the species’ repertoire (Hobaiter & Byrne, 2011a). The final repertoire of an adult is shaped and modulated by social interactions, and adult repertoires are smaller than those of younger individuals (Hobaiter & Byrne, 2011a; Fröhlich & Hobaiter, 2018). Final adult repertoires will vary slightly among individuals, even of the same community, as each individual adult would have had different experiences that modulated their repertoire and gesture use (Hobaiter & Byrne, 2011a; Fröhlich & Hobaiter, 2018).

Future studies could investigate whether gesture usage and meaning varies systematically across populations within and among species. The presence of locally restricted gesture usages and meanings would suggest that these variables are socially acquired and perhaps even culture-dependent in this restricted sense – even if their forms are not.

Ontogenetic ritualisation has also been proposed as a mechanism of gestural acquisition, particularly within dyads (Call & Tomasello, 2007; but see Genty et al., 2009; Hobaiter & Byrne, 2011b). Ontogenetic ritualisation involves the unintentional shaping of previously non-communicative behaviours into increasingly ‘ritualised’, communicating gestures through repeated social interactions with others (Tomasello & Call, 2019). Supporting this hypothesis, Halina, Rossano & Tomasello (2013) found evidence of gestural variation between mothers and infant bonobos and between mother–infant pairs, which was interpreted as evidence supporting the ontogenetic ritualisation hypothesis. Fröhlich, Wittig & Pika (2016) found between-sites differences in the gestures used by mothers and infant chimpanzees to initiate travel. However, Schneider, Call & Liebal (2012), found that chimpanzee and bonobo infants were more likely to use similar gestures as peers of the same age class, including across institutions, than the gestures of their mothers. Indeed, there also exists the possibility that different types of gestures are acquired via different mechanisms (Liebal, Schneider & Errson-Lenbeck, 2018). Whereas ours and previous results suggest that most great ape gestural forms are not dependent on copying (Byrne et al., 2017), in a few cases, gestural forms could be socially negotiated such as gestures performed in the context of mother–infant dyads to request transport, play or grooming (Bard et al., 2014; Liebal et al., 2018). This would still not require form copying, but it would involve a more central role of social learning in gestural acquisition.

(5) Implications of the Method of Local Restriction for conservation

Although it is clear that social interactions contribute to the patterns of expressed behavioural repertoires in great apes, the literature search of potential culture-dependent forms we undertook demonstrates that latent solutions are the rule rather than the exception: most behavioural forms across domains are not locally restricted and can therefore likely be individually re-innovated by naive individuals (captive and wild) in unconnected populations. The fact that we found a few (5) locally unique behaviours leaves open the possibility for copying social learning to play a role, especially in the acquisition of these three forms. Their geographic isolation, as well as their possible dependence on copying social learning, implies that these behaviours are the most likely forms susceptible to disappearing – perhaps forever – if the
populations in which they are present are decimated or completely destroyed. A recent study has suggested that populations with the highest behavioural diversity should be protected as “cultural heritage sites” (Kühl et al., 2019). Although we definitely support Kühl et al. (2019) in their efforts to increase the protection of great ape populations, we believe that behavioural diversity in and of itself should not automatically prioritise the protection of one ape population above another. It is possible that even very diverse behavioural forms can entirely re-appear in other populations. Instead, we argue that conservation programmes with the goal of protecting ape cultures should also focus on locally restricted behaviours. After all, it is these that are the most likely to be potentially dependent on copying social learning (Table 2) and therefore unlikely to be individually re-innovated in the same form in other populations. As such, these forms are the most susceptible behaviours to disappear due to human impact. In our view, the presence of the largest number of such behaviours in a population should be an important criterion towards prioritising the protection of its members. This is especially true if, during future latent solution experiments, these behaviours fail to be re-innovated and evidence is found of their reliance on form copying.

VIII. CONCLUSIONS

(1) Our results suggest that there exists a common framework to explain how most ape cultural behavioural forms are learnt by naïve individuals. Most ape behavioural forms are socially mediated latent solutions whose forms can be individually learnt. Consequently these forms reappear in culturally unconnected populations (sometimes even across different species of great apes). While the form (the know-how) of these behaviours and artefacts is not copied, non-copying variants of social learning (including transmission of know-what, know-where and other knowledge types such as know-when, who, etc.) play an important role in ape cultures by determining how frequently certain behavioural forms appear and are maintained in a given population. These various non-copying social learning mechanisms can provide and even transmit certain types of information that fuel the regular and reliable re-innovation of similar forms in other connected individuals. Whereas our data support the notion that most ape forms are socially mediated latent solutions, it remains possible that there exist rare exceptions whose forms rely on copying.

(2) Using the Method of Local Restriction, we present a list of locally restricted and locally unique behaviours in great apes across domains and species that stand as the most likely candidates for culture-dependent forms. These forms represent, to date, the most likely behavioural forms that might involve, or even require copying social learning. Although copying social learning (transmitting know-how) is not the only process involved in cumulative culture (novel inventions and change-inducing processes that increase behavioural complexity and/or efficiency are also required), cumulative culture cannot take place without copying mechanisms. Without copying, behavioural forms would slip back to causally transparent baseline levels at each transmission step, preventing behavioural forms (or know-how) from ratcheting. Identifying locally restricted or locally unique forms in great apes represents an indirect approach to identifying copying social learning mechanisms in these species by highlighting the most likely cases of culture-dependent forms. However, we found that these candidate cases were rare (and may be false positives).

(3) To determine conclusively whether any of the candidate culture-dependent forms detected by the Method of Local Restriction involve copying social learning mechanisms, these forms need to be tested for their reliance on copying in controlled experiments. If truly reliant on copying, culture-dependent forms should resist re-innovation in baseline tests but should be expressed by form-naive individuals after demonstrations. This information can also be derived from natural experiments, i.e. from observations of these forms in wild or captive ape populations.

(4) The Method of Local Restriction should also be applied to the archaeological record to examine whether behaviours associated with early hominins relied on copying social learning for their acquisition. A starting point could be to investigate whether certain stone tool production, transport and procurement techniques, stone tool typologies and stone tool uses occur in a single population of a single hominin species (which has been questioned in the past; Tennie, 2019a). Finding behavioural forms that could be specific to a single population of a species of early hominins could identify candidate cases of culture-dependent forms in our lineage. At the same time, such locally unique behaviours could delimitate possible timeframes where copying social learning abilities evolved in our lineage.

(5) The Method of Local Restriction should also be applied to other taxa such as cetaceans, corvids and monkeys to identify the most likely cases of behavioural forms that might be transmitted via copying in these species. As in the case of apes, these candidate forms would then need to be targeted in follow-up studies both with wild and captive populations (where applicable). We suspect that some cases of locally unique forms could be found in some animal species.

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XI. Supporting information
Additional supporting information may be found online in the Supporting Information section at the end of the article.
Table S1. Compiled results of studies reporting gestural repertoires in great apes.
Table S2. List of behaviours analysed.

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