Why do chimpanzees have diverse behavioral repertoires yet lack more complex cultures? Invention and social information use in a cumulative task

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Humans are distinctive in their dependence upon products of culture for survival, products that have evolved cumulatively over generations such that many cannot now be created by a single individual. Why the cultural capacity of humans appears unrivalled in the animal kingdom is a topic of ongoing debate. Here we explore whether innovation and/or social learning propensities may constrain the ability of one of our closest living relatives, chimpanzees (*Pan troglodytes*), to master an extractive foraging and tool-use task designed to afford opportunities for cumulative culture to develop. We further explore the potential demographic characteristics associated with novel task solutions. Chimpanzees (*N*=53) were inventive, flexibly exploring the novel task, albeit complex inventions were rare and shaped by prior individual experience with similar tool-use tasks. However, they displayed no evidence of cumulative cultural learning. Communities displayed richer behavioral repertoires and had greater task success than chimpanzees tested in an asocial control condition, but their solution complexity did not surpass what individuals invented. The lack of social transmission of complex and beneficial solutions in contexts like those we studied provides one explanation for the limited cumulative culture observed in this species.

Keywords: culture, cumulative culture, cumulative cultural evolution, innovation, social learning, tool use

1. Introduction

Homo sapiens displays unusual dependence upon culture for survival. This has culminated in the capacity to accumulate increasingly complex cultural traits that evolve through history, synonymously termed ‘cumulative cultural evolution’ or ‘cumulative culture’. It is this process of adding and refining new innovations (as well as old ones), and the social spread of these through populations and generations, that is seen by many authors as foundational to humanity’s global success as a species (Henrich, 2015; Henrich & McElreath, 2003; Tomasello, Kruger & Ratner, 1993). However, despite the adaptive benefits of cumulative cultural evolution, and the fact that many nonhuman animals (henceforth ‘animals’) display socially transmitted group-typical behaviors or “cultures” (Laland & Hoppitt, 2003; Laland & Galef, 2009; Vale, Carr, Dean & Kendal, 2017; Whiten, 2017), with many more being capable of at least learning from others (‘social learning’: Hoppitt & Laland, 2008), the cultural capacity of humans appears unrivaled.

What underpins the differences in humans and other animals’ cultural sophistication has been the subject of considerable debate (Dean et al., 2014; Osiurak & Reynaud, 2020). Many have suggested that animals lack some evolved, specialized socio-cognitive mechanism that make humans expert copiers and users of social information (Dean et al., 2012; Herrmann et al., 2007; Tennie, Call & Tomasello, 2009). Other authors highlight that animals may not be as innovative as humans, which may explain why cultural change is not as prevalent (reviewed in Dean et al., 2014; Osiurak & Reynaud, 2020; Whiten et al., 2003). Here, we directly appraise these proposed constraints on cumulative culture in chimpanzees, one of our closest living relatives. Specifically, we examined the use of innovation and social learning, both essential for cumulative cultural evolution, in a task in which progressively high-valued rewards could be accessed using correspondingly more complex solutions, thereby allowing for a potential cumulative building of skills.

Social learning provides a relatively economic source of information that allows the rapid acquisition of adaptive behaviors by otherwise naïve individuals, whilst avoiding the costs associated with individual exploration (e.g., time, energy, and risk to survival) (Kendal, Coolen & Laland, 2009). Research with non-human primates (henceforth “NHP”), particularly chimpanzees, due to their close phylogenetic relationship with humans, has focused intensively on the hypothesis that NHPs may have limitations in the nature of their social learning processes (e.g., Galef, 1992; see Dean, Vale & Whiten, 2018; Whiten & van de Waal, 2018 for reviews). This hypothesis has been only partially supported by resulting evidence. Many reports show that NHPs socially transmit behaviors which, in some species, generate behavioral traditions (e.g., Whiten et al., 1999; see Vale, Dean & Whiten, 2018 and Whiten & van de Waal, 2018 for reviews). Behaviors in NHPs, for example, can diffuse through matrilines (Lonsdorf, 2005; van de Waal, Bshary & Whiten, 2014), or be adopted by new group members following their migrations (Luncz & Boesch, 2014; van de Waal, Borgeaud, & Whiten, 2013); they can spread through groups when artificially seeded by a trained model (Hopper, Schapiro, Lambeth

& Brosnan, 2011; Watson et al., 2017; Whiten, Horner & de Waal, 2005), and lead to traditions lasting thousands of years (Falótico, Proffitt, Ottoni, Staff & Haslam, 2019; Mercader et al., 2007; Mercader, Panger & Boesch, 2002). At the same time, social learning experiments comparing humans and NHPs have highlighted species differences which show that traits spread more rapidly and faithfully in the former, which may help explain the cultural gap between humans and NHPs. Chimpanzees, although capable of social learning, tend to show a greater reliance on personally rather than socially acquired information compared to humans (e.g., Horner & Whiten, 2005; Vale et al., 2017a; Vale et al., 2017b; van Leeuwen, Call & Haun, 2014; though see Watson et al., 2018). When using social information, chimpanzees also often copy with less accuracy than humans (Vale et al., 2017a; Dean et al., 2012; Horner & Whiten, 2005), learning through processes such as emulation and end-state copying rather than teaching or imitation (e.g., Ebel, Schmelz, Herrmann, & Call, 2019).

In addition to social transmission, cumulative culture requires beneficial modifications and discoveries to occur. Populations containing individuals who learn through mixtures of personal experience and social learning benefit, because the former facilitate the transmission of up-to-date information that is essential in changeable environments (Kameda & Nakanishi, 2003; Rogers, 1988). However, despite the importance of innovation in cumulative culture, less is known of NHPs' innovation capabilities than their social learning abilities, which has been the primary focus of research to date, a bias recently argued by Osiurak and Reynaud (2020) to be unwarranted. Whether NHP's modest cultural complexity and diversity may be a result of infrequent innovation and trait refinement thus remains open to question.

The limited studies that have addressed NHP innovation have begun to chart the types and complexity of innovations made, often in foraging contexts (Reader & Laland, 2001). One line of evidence comes from long-term observations of wild populations which have identified behaviors not previously witnessed by researchers, suggesting they may have been innovated during the observation period. Examples include the recently observed community specific combinations of techniques involved in termite-fishing, suggestive of accumulative culture (Boesch et al., 2020), and the serendipitous discovery of 'moss-sponging' behavior; an apparent modification of 'leaf-sponging' in the Sonso chimpanzee community (Budongo forest; Gruber et al., 2015; Holbaiter et al., 2014).

Controlled experiments provide an important, complementary means of examining innovation and behavioral flexibility in conditions where novelty can be experimentally controlled. Such investigations have revealed that apes are capable of innovating new solutions, but that they are also conservative, often requiring old solutions to be blocked before they explore new ones (Manrique, Volter & Call, 2013; Davis, Schapiro, Lambeth, Wood & Whiten, 2019; Davis, Vale, Schapiro, Lambeth, & Whiten, 2016; Lehner, Burkart & van Schaik, 2011; but see Harrison and Whiten, 2018). Others suggest that innovations of complex solutions are rare in apes (Dean et al., 2012; Hanus et al., 2011; Tennie, Call & Tomasello, 2009). Very few gorillas and chimpanzees, for example, solve the 'floating peanut task' that requires displacing a peanut by inserting water into the tube it floated in (Hanus et al., 2011), a task previously solved by orangutans (Mendes et al. 2007; also see Tennie, Call & Tomasello, 2010).

In sum, the evidence concerning chimpanzee's innovation and social learning abilities is mixed. Some studies demonstrate a degree of behavioral modification and change through innovation and/or social learning, at least when past behaviors become obsolete (Davis et al., 2016, 2019; Manrique et al., 2013; Vale et al., 2017c). Others document little (Harrison & Whiten, 2018; Vale et al., 2017a) or no evidence (Dean et al., 2012; Marshall-Pescini & Whiten, 2008), and the putative innovations observed in the wild are typically modest (Boesch, 1995; Gruber et al., 2015). Moreover, few studies have examined NHPs' innovation of increasingly complex solutions *and* the impact of social information on task success in a cumulative task. The question of whether chimpanzees can innovate increasingly complex solutions by themselves, and whether these may be socially transmitted to others to create the early stages of cumulative culture evolution, therefore, has begun to be explored in only a handful of studies to date (Dean et al., 2012; Harrison & Whiten, 2018, Vale et al., 2017c; van Leeuwen, Cronin & Haun, 2014).

To extend this literature, the present study aimed to explore (1) chimpanzees' cumulative learning abilities, (2) their innovation propensities, broadly defined as the use of a new behavior, or an existing behavior in a new context (Kummer and Goodall, 1985; Reader and Laland, 2003; see below for a discussion of how we define 'new behaviors'), (3) the impact of social information on innovation and task success, and (4) demographic characteristics, as well as past experiences with similar tasks that may be associated with innovation on a task designed to afford cumulative culture (Fig. 1). For chimpanzees to show cumulative learning we would expect social groups to display more complex solutions than their counterparts in an asocial control condition. As cumulative culture requires the social spread of solutions beyond what individuals can invent (Dean et al., 2014), we would additionally expect complex solutions invented by individuals to spread within social groups.

According to variant approaches in the literature, animal innovation can be defined as a novel behavior (i) occurring at the individual *or* population level (Hochberg, Marquet, Boyd & Wagner, 2017), (ii) that may be either accidental *or* learned (Carr et al., 2016), or (iii) become useful or have evolutionary relevance when transmitted to others in communities (see Carr at al., 2016, Ramsey et al., 2007; Bandini & Harrison, 2020; Hochberg, Marquet, Boyd & Wagner, 2017; Mesoudi, 2010). Accordingly, we defined innovation consecutively at three different levels, taking these criteria in the literature into consideration. First, at its broadest level, we defined individual *invention* as the first instance of an individual performing a novel behavior that they had not previously witnessed others perform. Second, we distinguished *repeated invention,* that required inventions to be reproduced by the inventor twice or more (excluding inferred cases of accidental or unlearned behaviors), so being counted as entering their repertoire, even if temporarily. Third, following authors such as Hochberg et al. (2017), we defined *innovations* as inventions reproduced by one or more conspecifics after witnessing the behavior (inferred transmission). Our intention was to explore the occurrence of individual invention, repeated inventions by individuals, and innovations in groups, as defined above, in the complex world of opportunities we presented to a large sample of chimpanzees.

2. Method

2.1. Participants

Forty-five (30 female) chimpanzees were tested in their eight social groups (social condition) and eight (four female) chimpanzees were tested individually (asocial condition). Chimpanzees in the social condition ranged in age from 14 to 54 years (mean = 33 years) and those in the asocial condition ranged from 21 to 38 years (mean = 30 years). Participants lived in social groups of between four and eight chimpanzees, each with access to enriched outdoor and indoor enclosures. Chimpanzees were housed at the National Center for Chimpanzee Care (NCCC) at the Michale E. Keeling Center for Comparative Medicine and Research. The NCCC is fully accredited by AAALAC-I. Chimpanzee participation in this study was voluntary. Three chimpanzees (two female) in the social condition did not interact with the task and were excluded from analyses. Nine of the chimpanzees (four in the asocial condition) had, in earlier studies, combined two components to make an elongated stick-like tool, or had combined a token cap and a token (Price et al., 2009; Vale et al., 2016; Vale, Flynn & Kendal, unpublished data) and all chimpanzees had prior exposure to food-filled pipe feeders that required probing with stick tools to extract food (e.g., Hopkins, Wesley, Izard, Hook & Schapiro, 1995). Ethical approval was granted for this study by the University of St Andrews' Animal Welfare and Ethics Committee and UTMDACC Institutional Animal Care and Use Committee (IACUC approval number 0894-RN01).

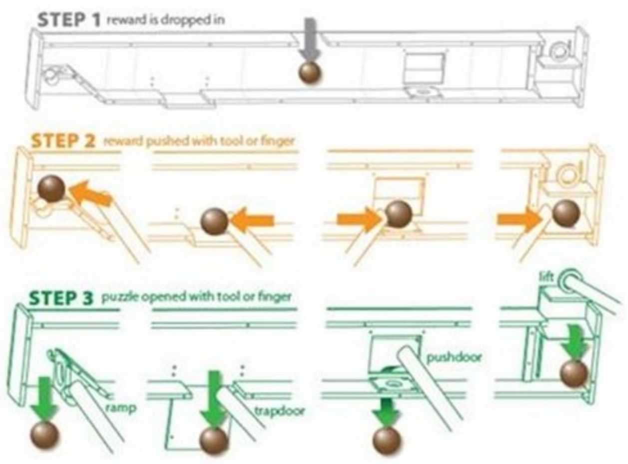

Fig 1. Schematic of four reward exits repeated on each task level (L1-L4). The centered reward could be maneuvered left and accessed via the trapdoor or ramp, or moved to the right and extracted through the pushdoor or lift

2.2. Apparatus

This study employed a large puzzlebox, named the 'Small World' (SW: see McGuigan et al., 2017 for a child version of the SW; direct species comparisons will be reported elsewhere: Vale et al., in prep). The SW incorporated four increasingly difficult levels (elongated boxes L1-L4; see Fig. 1) baited with increasingly preferred rewards ranging from a carrot piece at L1 to a more preferred strawberry at L4. Each box level included four reward exits; the ramp [R], trapdoor [T], pushdoor [P] and lift [L], towards which the reward could be maneuvered left or right from its initial central location (see Fig. 1). Once an exit was successfully opened, the reward fell and rolled down a slope that was angled towards participants, enabling its retrieval. The levels were placed at variable distances from the participants such that level 1 (L1) was close enough to be manipulated using the subject's hands and fingers (or a tool if preferred); level 2 (L2), was slightly farther away from the participant (10cm) and required the use of a stick tool to move the reward and open an exit; and level 3 (L3) was further back still (23cm) and required modified, elongated tools to reach it. Finally, L4, placed 23cm back, was modified so that chimpanzees had to create an elongated hooked tool to release the reward. Two types of tools were provisioned: yellow 'combine tools' and green 'unfold tools'. The 'combine tools' consisted of thinner components that could be inserted into the ends of thicker ones. One of these thicker components had a hook end for L4. A single thinner component could be used to manipulate L2 (and L1) without modification. The green 'unfold tools' consisted of hinged, initially folded tool components that could be unfolded to make a long tool. On the unhinged end of the 'unfold' tool a cuff was placed that had to be removed to permit unfolding (see Fig. 2). The 'unfold' tools also had a hooked end that, when unfolded, could be used to manipulate L4. Akin to the 'combine tools', we provisioned a green short tool that could reach L2 (and L1) without modification. We additionally provisioned an array of non-functional tools that were either too thick, flimsy or short to be reliably used to access the rewards (Fig. 2); thick, short PVC L-shape; flimsy straws; flimsy, long bamboo sections; short, black piping sections; and short sections of bamboo.

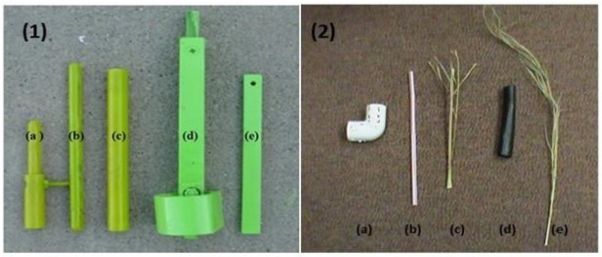

Fig 2. (1) Functional tools that could be combined (yellow tools) or unfolded (green tools). (1a) hook end that combines with (1b) the middle section long enough to reach L2 and (1c) the handle, to create an elongated tool. Combining (1a) and (1b) was required to reach L3 and adding (1c) for L4; (1d) folded tool with an un-foldable hook on one end and a cuff that had to be removed before its extension to reach L3 and L4; (1e) flat tool long enough to reach L2. (2) Non-functional tools; (2a) thick, short PVC L-shape pipe; (2b) flimsy straws; (2c) short sections of bamboo; (2d) short, black piping and (2e) flimsy and long bamboo sections

2.3. Procedure

Prior to running the study, all participants were given food preference tests to establish the desirability of different foods. Four food types were placed in four food wells atop a single tray (food locations were pseudo-randomized) and pushed within reach of participants. A participant selected one piece of food at a time until all four pieces were consumed, and their order of preference was documented. Five repetitions (trials) were presented per subject, all conducted in a group setting. Foods were ranked according to the frequency they were chosen first (all trials were pooled). After testing various food types, these tests established that carrot was the least preferred food (used for L1), followed by orange (L2), then apple (L3), and finally the most desirable food was strawberry (L4).

Chimpanzee groups were presented the task on consecutive week days for a total of eight hours across four, two-hour 'open diffusion' sessions (i.e. it was 'open' in terms of who worked at the task, who observed whom, and whether diffusion resulted). Sessions stopped prematurely if a part of the task was broken by the participants, which happened infrequently, and resumed once the task was fixed (usually by the following day). Sessions started once the task was baited with one reward for each level, and the tools were provisioned by pushing them through the enclosure mesh. Three of each tool-type were provisioned, with tools being replaced by new ones if they were transported >3m away from the task. Tools that were pushed outside the enclosure were immediately passed back through the mesh in their initial, unmodified states (e.g., uncombined sections and folded tools). For the first hour of open diffusion, each level was rebaited immediately following reward extraction to sustain initial motivation, increasing every consecutive hour by one-minute intervals until a maximum hiatus between reward retrieval and rebait reached five minutes for the final three hours of testing. This was done to facilitate potential attempts at the more difficult levels upon solving easier ones.

For the asocial condition, chimpanzees voluntarily separated from their groups for two 30-minute sessions. Thus, the eight chimpanzees in this condition received one hour of testing time and were collectively exposed to the task for eight hours. As these chimpanzees had no competition from groupmates during testing, we provisioned them with just one of each tool-type. Tools that were pushed out of enclosures were returned to participants in their unmodified states. Re-baiting for this condition was done in five-minute intervals (the final rebait time in the social condition), to permit exploration of the more difficult levels once an easier one was solved.

Sessions were recorded by a video camera. Videos were later coded and 15% were checked by a second coder. Inter-rater agreements for successful reward extractions (94% agreement), the level (L1-4; 97% agreement) and exit (98% agreement) used, and how rewards were extracted (hand or specific tool used; 98% agreement) were high. We coded all novel task solutions in relation to three differing definitions of 'innovation', classifying (i) *invention* as the first instance of individuals performing a behavior that they had not previously witnessed others perform (ii) *repeated invention* as inventions that were repeated more than once by the inventor, and (iii) *innovations* as inventions that transmitted to others in a community (witnesses of the behavior performed the same behavior). Chimpanzees were recorded as attending if they were within 1m proximity to and facing the task when a conspecific was extracting a reward. For our task, inventions were coded as occurring for each first success, including re-inventions by individuals that had not previously witnessed the behavior, at specific exit on a specific level made by a specific tool (including manual extractions). All four exit release mechanisms were unfamiliar to the chimpanzees, and although chimpanzees had some past tool experience such as dipping sticks into juice, the provisioned tools were also new to them, and different tools were required for different levels. We considered the type of tool used within these definitions given that wild communities show subtle cultural differences in the types of tools they use (e.g., stone vs wood anvils), how they use them, and in their modifications (e.g., leaf to moss sponges, innovation of brush tipped probes: e.g., Boesch et al., 2020; Luncz & Boesch, 2015; Luncz, Sirianni, Mundry & Boesch, 2019; Pascual-Garrido, 2019). All first successes by asocial controls were considered inventions as they could not copy others and as the task, exits, tools and exits were novel to them. Chimpanzees were allocated scores based on how many inventions, repeated inventions, and innovations they performed (frequency counts).

We were interested in which variables predict a chimpanzees' level of inventiveness, focusing on their age, group size, sex and dominance rank, as well as the impact of social information they had the opportunity to acquire. For example, low-ranking individuals may be more inventive and exploratory (Hopper et al., 2015), while dominant individuals may display more inventions that become innovations, due to biases in copying high-ranking individuals (Kendal et al., 2015). Following Kendal and colleagues (2015), dominance rank was assessed by using three chimpanzee experts' ratings using a three-point categorical dominance scale ranking each chimpanzee of each group as either 'high', 'medium' or 'low' dominance. As in Kendal and colleagues (2015), the modal rank was selected for the few cases of rank disagreements. As L3 and L4 could be solved by combining two or three tools (see Fig. 3), we were also interested in whether some chimpanzees' past tool combining history would predict the solving of these levels.

Fig 3. L3 reward being maneuvered using a combined tool

2.4. Statistical Analysis

Models were run using the Bayesian Rethinking R package (McElreath, 2016; 2019). Models were multilevel with varying intercepts (a 'random effect') fitted for individual and group identity to control for multiple data-points from individuals and groups. The models generated posterior estimates using the Hamiltonian Monte Carlo algorithm available in the rstan package (Stan development team, 2018). Chain convergence was assessed by visual inspection of traceplots, and 'Rhat' values that should equal 1 when convergence occurs (McElreath 2016).

Models were constructed using a Poisson distribution (and log link) appropriate for count data. Our response variables were; inventions, repeated innovations and innovations, as defined above. We constructed models that (i) examined the effect of participant characteristics on our response variables, including participant age (years), sex (females coded 0/males coded 1), tool combining history (no history coded 0/history of tool combining coded 1), group size (range 4-8) and dominance (low coded 0/medium coded 1/high coded 2). Age was z-transformed before entering it into the models to aid model interpretation.

We also explored whether testing in a social group influenced our response variables while controlling for task exposure time (limited to the first hour of testing for all individuals to make them comparable with the control condition). Here, community level inventions (the number of unique behavioral variants evident in each group, N=8 groups) were compared to the number of inventions made by asocial controls (N=8), by including social group as a predictor (asocial controls coded 0/social groups coded 1) and comparing this to a null model with the same structure, omitting this predictor. The second model compared community level successes (number of reward extractions) to successes of individuals in the asocial condition. Because we used group level and individual data, we did not include individual or group as random effects in these models.

For model comparisons, we used the Watanabe-Akaike information criterion (WAIC) as a measure of out-of-sample deviance. When models performed similarly, we report the outcomes of both models (McElreath, 2016). Multicollinearity between predictors was checked using 'pairsplots' in the 'rethinking package' and model fit to the raw data using the 'postcheck' function that plots model generated data against the raw data. Where necessary, model sampling efficiency, and chain convergence were improved by increasing the maximum allowed treedepth to 15 and "adapt_delta" values closer to 1. We report the posterior mean, standard deviation and the highest posterior density interval (89% HPDI) for predictor variables, on a log scale (effects of the predictor variable in relation to the response variable can lie either side of zero). HDPIs that cross zero were interpreted to indicate no clear effect of a predictor, or a (weak) effect if most of the density of the posterior lay on one side of zero.

3. Results

3.1. Chimpanzees' Novel Solutions in a Group Setting

Chimpanzees in the eight groups produced 140 inventions (19 of which were re-inventions by individuals who had not previously witnessed the behavior), with 27 participating chimpanzees doing so at least once. Inventions ranged from elementary manual reward retrieval acts from L1 exits, to combining three or four tool components to retrieve rewards from L3 and L4 exits. A total of 46 of these inventions involved manual reward extractions (33%) and 94 (67%) involved tool use.

Restricting the number of inventions counted to those that were repeated by inventors, so excluding some accidental or unlearned behaviors, reduced the number of inventions to 72 'repeated inventions' (51% of inventions were repeated by the inventor). This included individuals repeating 22 (48%) of 46 manual techniques displayed, and 50 (53%) of 94 tool techniques. Fig 4 illustrates the types of repeated inventions performed by groups and Fig 5 shows the total number of repeated inventions that were performed at each of the task levels.

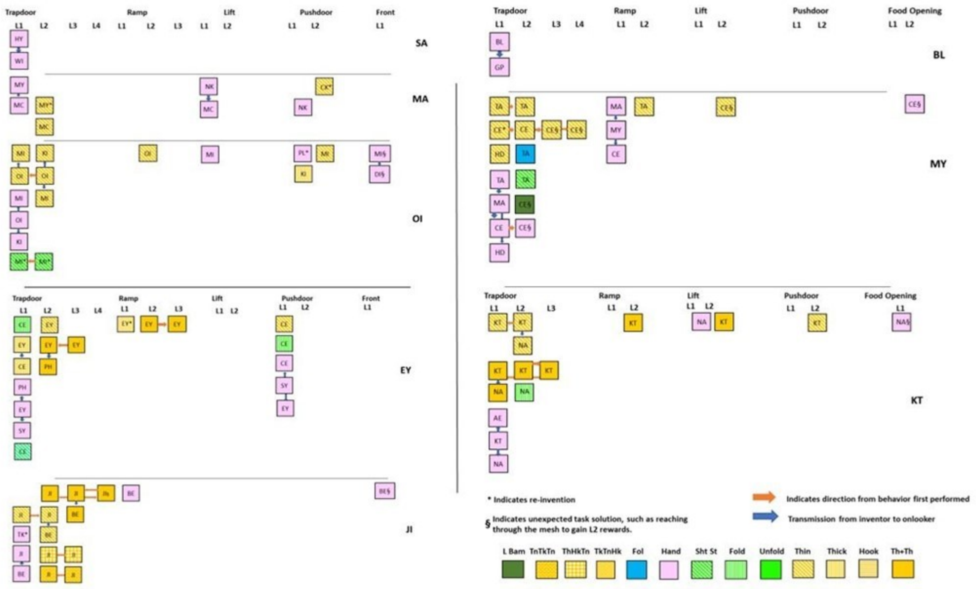

Fig 4. All instances of repeated inventions and of subsequent productions of the same tool-exit combination by others. Note: not all innovations are depicted as there are inventions that were not repeated but still spread to others; *re-inventions may be shown but not the original invention in cases where the first invention was not repeated by the original inventor. Group indicated by initials (e.g, JI and EY). Defining terms: L. Bam = Long bamboo; TnTkTn = Thin section combined with Thick section combined with Thin; TkTnHk = Thick section combined with Thin section combined with Hook; Fol = Foliage; Sht St = Short Straight section; Fold = Folded tool; Unfold = Unfolded tool, Th+Th = Thick section combined with Thin section.

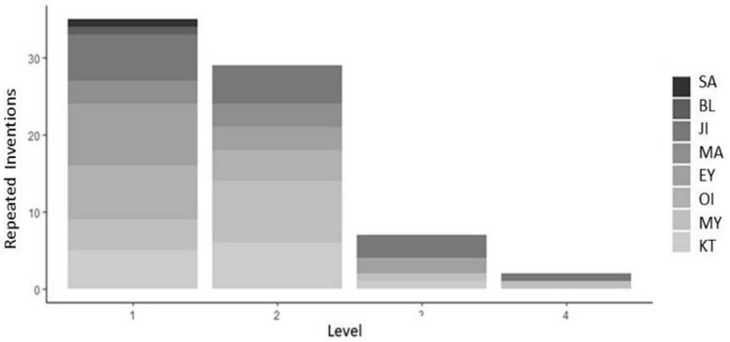

Fig 5. The number of repeated inventions made at each task level. Shading indicates social group (8 groups)

Just 27 inventions' (19% of inventions) were then reproduced by others who had previously witnessed the behavior, consistent with community spread (although we cannot rule out learning by reinvention). Inventions that involved more simplistic manual extractions were reproduced by onlookers as 'innovations' more readily (16 of 46 manual extraction techniques, or 35%) than were tool extraction methods (just 11 of 94 tool behaviors, or 12% were reproduced). All manual innovations were at the lowest task level (L1, as tools were required for L2 up), whereas tool innovations included 5 at L1, 5 at L2 and just 1 at L3.

Turning to who the inventors were, the 'participant characteristics model', returned very similar, but slightly higher estimated out-of-sample deviances to our null model (Table 1, Ns=42 chimpanzees tested in group settings in both models). Cautiously interpreting the results for the full model, sex was found to have a weak effect on invention, with males inventing less often than females (Table 1). Older individuals also tended to invent solutions less frequently than younger ones, whereas chimpanzees with prior experience of tool combining were more inventive than chimpanzees lacking this experience (31 inventions, performed by 5 chimpanzees, relied on combined tools, with two of these involving an individual using a tool previously made by an experienced combiner). There was however no effect of group size or dominance on individual inventions. Finally, we note that our models showed individual variation in chimpanzee invention levels (mean = 0.64. SD = 0.14, HDPI = 0.44, 0.90), and a small amount of group level variation (mean=0.19, SD = 0.16, HDPI = 0.02, 0.48).

Table 1. Model comparisons reporting WAIC for the full and null 'participant characteristics' models. The posterior means, standard deviations and 89% HDPIs are reported for each fixed effect.

Participant Characteristics and Invention

Model	WAIC	Fixed Effect	Posterior Mean	SD	HDPI Lower 5.5%	HDPI Upper 94.5%
Null	151.9					
		Age (Older)	-0.52	0.29	-0.97	-0.05
Full	153.3	Group Size (Larger)	-0.15	0.14	-0.38	0.07
		Sex (Male)	-1.03	0.53	-1.88	-0.20
		Tool Experience (Yes)	1.42	0.60	0.47	2.38
		Dominance (High)	0.26	0.34	-0.27	0.80

Participant Characteristics and Repeated Invention

Model	WAIC	Fixed Effect	Posterior Mean	SD	HDPI Lower 5.5%	HDPI Upper 94.5%
Null	122.5					
Full	119.0	Age (Older)	-0.65	0.31	-1.14	-0.16
		Group Size (Larger)	-0.18	0.14	-0.42	0.04
		Sex (Male)	-1.51	0.58	-2.45	-0.61
		Tool Experience (Yes)	1.62	0.61	0.65	2.60
		Dominance (High)	0.18	0.36	-0.39	0.75

Participant Characteristics and Innovation

Model	WAIC	Fixed Effect	Posterior Mean	SD	HDPI Lower 5.5%	HDPI Upper 94.5%
Null	100.3					
Full	88.2	Age (Older)	-0.44	0.31	-0.94	0.02
		Group Size (Larger)	-0.31	0.15	-0.57	-0.09
		Sex (Male)	-1.46	0.62	-2.50	-0.53
		Tool Experience (Yes)	1.09	0.59	0.16	2.01
		Dominance (High)	0.56	0.39	-0.03	1.20

Turning to repeated inventions (see Fig. 4 & 5), consistent with individual learning of an invention, our full model returned only slightly better out-of-sample predictions (WAIC = 119.0, N=42) than our null model (WAIC = 122.5, N=42). Our full model revealed very similar effects as our previous model focusing on the more inclusive definition of invention, with older and male individuals performing repeated inventions less frequently than younger and female chimpanzees. Again, there was a positive effect of complex tool combining experience on repeated invention frequencies (17 repeated inventions involved a combined tool, performed by 3 chimpanzees).

In analyzing characteristics that may potentially be associated with our most restrictive definition, ‘innovation’, we found the full model returned better estimated out-of-sample deviance (WAIC = 88.2) than the null model (WAIC = 100.3; Ns=42 chimpanzees tested in group settings in both models). The full model showed a positive effect of tool combining history and negative effects of age and gender (males performing worse than females; Table 1). Unlike our previous models, there was some indication that dominance had a positive effect on innovations, such that the inventions of higher-ranking individuals were more readily reproduced by onlookers than those shown by lower-ranking individuals.

3.2. The impact of the Social Group context on Invention

To examine the potential role of social facilitation on chimpanzee invention, differences in invention propensities between communities and asocial controls were explored. For these models we used the community level behavioral repertories (N=8 groups) seen in the first hour of testing, comparing them to the behavioral repertoires of the asocial controls (N=8 individuals) with no random effects entered. Our full model (WAIC = 88.5), that included social group as a predictor returned better out-of-sample predictions than our null model that excluded this predictor (WAIC = 108.8). Being in a social group (coded 1/asocial coded 0) had a positive effect on the number of inventions made (posterior mean = 1.41, SD = 0.32, 89% HDPI = 0.92 ,1.93), with our model predicting communities averaging 4.32 more inventions than asocial controls (mean number of inventions for asocial controls = 1.5 (raw data)). This suggests social facilitation may have had a modest but significant effect on chimpanzees' early exploration of the task.

3.3.The Impact of the Social Group context on Task Success

We ran similar analyses to those described above, but this time considering whether communities had greater task success (reward extractions) than asocial controls during the first hour of testing. Our full model (WAIC = 304.5) improved the out-of-sample deviance compared to our null model (WAIC = 556.0). Being in a social group had a positive effect on the task success of communities (posterior mean = 2.42, SD = 0.2, 89% HDPI = 2.10, 2.76), with groups averaging 11.47 more successes in the first hour of testing than did asocial controls (mean = 3.13 (raw data)), despite the potential for competition over access to the task in groups. However, group tested chimpanzees did not surpass asocial controls in the complexity of their solutions in the first hour of testing; a requirement for cumulative culture. In fact, the only chimpanzee that successfully created and used a combined tool to extract a L3 reward during this time was a female asocial control individual

3.4.Solution Complexity and Progress over Time

Though groups were more successful, and displayed richer behavioral repertoires than asocial controls, to offer any evidence of cumulative learning, groups must increase their solution complexity over time. Each level of the SW was designed to be more challenging than the last, requiring an escalating series of actions (all tool-based, for L2-L4) to achieve success. This was reflected in our results, with 29 of the 42 (69%) chimpanzees in groups retrieving 739 carrot pieces from the most basic level (L1), 20 (48%) retrieving 471 orange pieces from L2 (requiring simple tool use) and just 4 (10%) retrieving 177 apple pieces from L3 by making or using a combined tool (three further individuals solved L3 by reaching through the mesh or collecting long pieces of foliage from their enclosures). Six strawberries were also extracted from L4 by three individuals through unexpected behavioral inventions which provide further documentation of chimpanzees' inventiveness. Two of these chimpanzees discovered they could bypass the hook requirement, by carefully using a combined tool to apply pressure to the bolt attaching the loop to the ramp (the release mechanism), rotating it downwards to release the reward. The second method discovered by a male involved inserting a combined tool into L4 and leveraging the tool to open the trapdoor. Lastly, one chimp with particularly small arms also used this method but by reaching through the mesh with an unmodified tool. Typically, easier levels were solved prior to the more difficult ones: just six of the group tested participants ever solved L2 prior to L1, and none of these chimpanzees solved L3 without first solving L1 and L2. Just one asocial control individual solved L3 without first solving L2; Fig. 6 shows the percentage of rewards received from each level in each successive test hour).

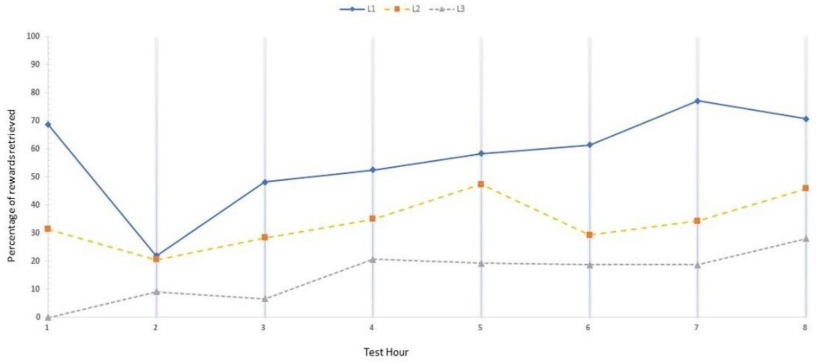

Fig 6. Percentage of available rewards retrieved at each level in each successive test hour. The number of rewards available each hour was calculated by dividing the duration of the session (60 mins) by the re-baiting schedule of that session (1-5 mins)

3.5.Did Complex Solutions Spread within Groups?

Five groups contained a chimpanzee that had previously combined different tools, providing a 'self-seeded' model for others copy. As cumulative culture requires the social transmission of increasingly complex solutions, we were interested in whether 'self-seeded' groups would outperform those that lacked a potential model. Despite three of the experienced tool users combining tools to extract rewards from the task, the behavior did not spread within their respective groups. Specifically, only one individual extracted a reward from L3 using a combined tool, one that was pre-made by an experienced tool combiner (two more used an already combined tool on lower levels), and two individuals (one from a group without an experienced combiner) made a combined tool but failed to use it on the task. We could not statistically compare successes at L3 between those that had and had not witnessed reward extractions using elongated tools as performances were at floor level; only one witness ever solved L3, and no chimpanzee did so in the absence of an experienced combiner.

4. Discussion

4.1. Cumulative Culture

We examined chimpanzees' inventiveness and the impact of social information on success at a cumulative task. Out of the 42 chimpanzees tested in groups, L1, L2, and L3 were solved by 29, 20 and finally just four individuals, respectively, with easier levels typically solved prior to the more difficult ones. This suggests there was cumulative learning at an individual level. However, we found no evidence for cumulative *cultural* learning that implicated a role for social learning. When controlling for test time, chimpanzees tested in groups failed to perform behaviors that were more complex than the inventions of control individuals tested alone. Chimpanzees also showed no evidence of learning to make elongated tools from conspecifics who became proficient in the behavior to gain the L3 desirable rewards, and any cumulative progress made over time in the percentage of rewards retrieved from this level was underpinned by just four individuals (Fig 6). In contrast, inventions, defined as the first occurrence of a unique exit/tool/level combination by individuals that had not previously witnessed the act, were relatively common, with over half of the chimpanzees tested in a group setting performing a behavior novel to them at least once. However, the invention of creating elongated tools to solve L3, building upon unmodified tool use, was rare and largely determined by chimpanzees' experience with making similar tools in the past (three or more years ago) (Price et al., 2009; Vale et al., 2016). The data thus suggest that chimpanzees engaged in *individual*-level skill scaffolding, where progress required some acquired knowledge of similar, easier behaviors, as opposed to cumulative cultural learning which requires alternation of individual inventions and social spread of the results, generating increasingly complex behaviors (Whiten, 2017).

These results are in line with studies that found no clear evidence for cultural ratcheting in captive chimpanzees (Dean et al. 2012; Marshall-Pescini & Whiten, 2008). Our results offer some clarification as to why cumulative learning may be lacking in these controlled experiments. Most striking were the findings that, even though chimpanzees made simple, beneficial modifications to an existing behavior (with tool use building on manual reward extractions), the social spread of tool *modifications* to others was mostly absent. This is consistent with the hypothesis that captive chimpanzees are unlikely to copy behaviors that are more elaborate than their currently favored ones (Dean et al., 2012; Gruber et al., 2009; Marshall-Pescini & Whiten, 2008; Tennie, Call & Tomasello, 2009). Such difficulty in, or disinclination to copy, some new or hard-to-invent behaviors poses a constraint, as adaptive discoveries will become lost, impeding cultural evolution. This contrasts with findings from human populations, who regularly show a heavy reliance on social learning (e.g., Carr, Kendal & Flynn, 2015; Flynn, Turner & Giraldeau, 2016; Nielson & Tomaselli, 2010) and who can acquire relatively novel, complex behaviors with high fidelity (e.g., Dean et al., 2012; Derex, Godelle &

Raymond, 2012; Derex et al., 2013; McGuigan et al., 2017; van Leeuwen et al., 2018). Such differences in the willingness or ability to use social information in this context may be important in explaining the extent to which some humans and chimpanzees display cumulative cultural evolution (Dean et al., 2014; Tomasello, 1994; Tennie, Call & Tomasello, 2009; van Leeuwen, Call & Haun, 2014). However, we cannot definitively rule out other contributing factors, such as failure to adopt a higher-paying behavior due to satisfaction with a lower paying option (e.g., L2) (Marshall-Pescini & Whiten, 2008; Vale et al., 2017c), a general difficulty with combinatory acts (see Vale et al., 2017 for evidence of social acquisition of tool *deconstruction*), or the age of our sample exceeding any 'sensitive learning period' during which combinatory tool technologies may be learned (Inoue-Nakamura & Matsuzawa, 1997; Matsuzawa, 1994; Biro et al., 2003). Further research with more diverse human and chimpanzee cultures will be needed to discover if this difference in the extent social information is used to propagate new and complex behaviors generalizes to a true species-level difference (see Henrich, Heine & Norenzayan, 2010 and Webster & Rutz, 2020).

We note, however, that provisioning multiple tool, exit and level options may have encouraged reliance on asocial information, as these multiple options afforded task access to more than one chimpanzee at any given time. This may have encouraged individual exploration of exits, levels and tools that were not in use by others at that time. Competition over access to higher levels between chimpanzees that solved L3 and conspecific witnesses could also have inhibited the spread of these complex behaviors in groups. However, L3 solvers did not interact with the task for the full duration of all sessions, allowing others to access L3 in their absence, and making this explanation less likely.

4.2. Inventions, repeated inventions and innovations

Chimpanzees discovered many novel solutions (n=140), with groups varying in the richness of the array of inventions they displayed (3-27 per group, overall group mean = 17.5). Chimpanzees explored a considerable proportion of the potential maneuvers embedded in the SW. Opening amongst the 16 potential exits was achieved for levels 1-4 of the trapdoor and ramp, 1-2 of the lift and 1-3 of pushdoor, leaving only three exits undiscovered. Both types of tool, combine and unfold, were used, including a variety of combinations in the case of the combine options. Whereas inventions were common in groups, their presence in other group members (indicating probable social transmission) were relatively rare (n=27), and idiosyncratic inventions were often transitory (repeated inventions: n=72), disappearing from the inventor's repertoire after their initial discovery. A similar trend has been observed in wild chimpanzees, where newly observed behaviors were common but only around a third of them appeared in other community members (Nishida et al., 2009). These findings suggest that individual discoveries can quickly become lost, as others fail to acquire them.

4.3.The impact of social information

Fewer inventions occurred in the control chimpanzees, with just three (of eight) displaying a combined total of 12 inventions. Controlling for test time, chimpanzees in social groups displayed richer behavioral repertoires, and extracted more rewards, than these asocial controls. This suggests that access to social information, while not facilitating cumulative culture, afforded benefits to groups. This may in part reflect a social facilitation effect (Zajonc, 1965) in which activity at the SW by group members stimulated a similar focus by others, and in part a larger pool of diverse motivations and cognitive dispositions across the groups (Griffin & Guez, 2015). The significance of the diversity of invention for culture displayed by the chimpanzees is that it provides 'raw material' that can potentially spread to others via social learning to seed population-level innovations.

The behavioral diversity in asocial controls could have been curtailed by their rebaiting schedule occurring at five-minute intervals, compared to immediately for group tested participants at the start of the study. The longer rebait delay meant that subsequent to consuming a lower level reward item, asocial controls could not immediately explore other means to extract low value rewards, which continued to be available to groups. Though we recognize this potential confound, we chose different reward schedules in order to best pursue our interest in determining what asocial controls were capable of in their necessarily shorter task exposure time (our focus for cumulative culture meant we were firstly concerned with differences in group/individual trait complexity before differences in diversity). In practice, only three of eight asocial controls experienced this five-minute interval, two of which proceeded to explore, and extracted rewards from other levels during this time. This suggests that the rebaiting schedule did not in fact inhibit exploratory behaviors in our control individuals.

4.4.Solution complexity

Despite its high prevalence, invention was particularly associated with two factors; solution complexity and an individual's experience with similar tool-use behaviors. Concerning solution complexity, most innovations were relatively simple, occurring at L1 and L2. Complex combinatory tool construction, by contrast, were rare, and tied to chimpanzees' past experience with similar tool-based tasks. Combinatory tool manufacture, therefore, is best explained as an application of a known behavioral routine to new stimuli and contexts. Such findings are reminiscent of those concerning innovations in wild populations, where these often represent behavioral generalization to new materials and contexts (e.g., moss sponging and leaf clipping; Boesch, 1995; Gruber et al., 2015).

Invention of L3 and L4 solutions may have been constrained for multiple reasons. One pertains to L3 and L4 representing what has been identified as an 'ill structured problem' (Cutting et al., 2014). In this, process information concerning how to reach the end goal from the start state ('how knowledge') was missing. Thus, participants had to infer that solutions required a state change to the tools provisioned (elongation and hook creation). Even young human children perform very poorly in such contexts, for example failing to bend a pipe cleaner provided to make a simple hook to extract a prize from a narrow jar (Cutting et al., 2014), and chimpanzees may have experienced similar difficulty in recognizing potential tool affordances. This does not explain, however, why the chimpanzees that *were* provided 'how' information by conspecifics solving L3, failed to copy and reach this level.

Alternatively, invention could have been hindered by the combined complexity of what individuals already knew and what a cumulative step up would entail. Davis et al. (2016, 2019) showed that chimpanzees appear to transition more easily to new behaviors if behavioral approaches to the problem already existing are relatively simple, than when such known behaviors are already relatively complex. The latter context requires inhibiting a technique that may have been achieved by considerable effort or practice, and evolution may have shaped a mentality adaptively reluctance to abandon well-rehearsed techniques in this circumstance. Similarly, Davis et al. (2019) found a reluctance to progress from complex to other complex acts, compared to a simple-to-simple transition, with the former entailing a risk of additional effort when a well-tried routine was already known to work. Such inhibitions might explain chimpanzees' readiness to progress from L1 to L2, but more rarely from L2 to L3 when tool construction was required (c.f. Hrubesch, Preuschoft & van Schaik, 2009; Marshall-Pescini & Whiten, 2008).

Finally, the types of tool modifications required for this study may have impeded cumulative learning. Although chimpanzees' fashion many kinds of tools in the wild (Boesch and Boesch 1993; McGrew 2010), this is typically via broadly destructive actions, like stripping leaves from a stem; tools are rarely constructed by combining two or more objects (although several may be used consecutively in a 'tool kit': e.g., Martin-Ordas, Schumacher & Call, 2012 and Sanz & Morgan, 2007). One explanation for the lack of success at L3 might be that chimpanzees have some inherent cognitive limitation conceiving of tool construction that constrains both their individual inventiveness and ability to socially learn about such actions. Such a constraint might parallel the apparent inability of many primates to either invent the use of stick or hammer tools *per se* or learn to do so by observation (e.g. Zuberbuhler et al. 1996; Bandini and Tennie 2018). Accordingly, complex tool detachments and subtractions, rather than addition or combination of elements, may be more ecologically valid behaviors to pursue in future work (e.g., Vale et al., 2017c). If a specific limitation in the invention and cultural transmission of technologies that involve construction explains our results, that may be significant in understanding the contrast with human cumulative technological culture, so much of which depends on this very characteristic.

4.5. Participant Characteristics and their association with Inventions, Repeated Inventions, and Innovation

There was some evidence to suggest that novel behaviors, across all our measures (inventions, repeated inventions and innovations), were performed more frequently by females than by males. Although caution is required in interpreting the effect of sex from our small sample, there are similar reports in wild populations, implicating female NHPs as the more inventive sex (Kawai, 1965; Kummer & Goodall, 1985; although see Reader & Laland, 2001). In terms of our task, that female chimpanzees use tools more frequently and with greater proficiency, and from an earlier age, than males (Boesch & Boesch, 1981; Krummer & Goodall, 1985; Lonsdsorf, 2005; McGrew, 1979; Pruetz et al. 2015; Hopkins, Reamer, Mareno & Schapiro, 2015) may have facilitated inventions by enabling them to access more solutions available at higher task levels (L2). Should females be the more exploratory sex (although see Reader & Laland, 2000), with a proclivity to rely more on social learning (Lonsdorf, 2005; Watson et al., 2018; see also Brand, Brown & Cross, 2018 and Cross, Brown, Morgan & Laland, 2016 for human cases; but see Frick, Clement & Gruber 2017), this may go some way to explain why the number of cultural traits in populations of chimpanzees has been found to positively correlate with the number of females in a community, and not males (Lind & Lindenfors, 2010).

We also found that younger adult individuals were more inventive and innovative than older individuals, as has been documented in wild populations (Biro et al., 2003). Older captive chimpanzees show reduced movement relative to younger individuals (Baker, 2000), and it is possible that physical impairments (e.g. joint stiffness) limited tool use and exploration of the task space in this study, as well as their motivation levels. Cognitive deficits, as seen in aging humans (e.g., see Li, Lindenberger & Sikström, 2001) may also play a role, although there is very little evidence for age-impairments on similar physical responses, including on tool and fine motor ones, at least in female chimpanzees (Lacreuse, Russell, Hopkins & Herndon, 2014). There is very little data available on this topic however, and our findings suggest aging effects could be an interesting avenue to pursue. This is especially so given biases of youngsters to observe actions in others of the same age, or older in this species (Biro et al. 2003).

We saw no effect of dominance on who initially solved the task (inventions) or who went on to repeat their own inventions. This was surprising given that a largescale review concluded that low-ranking individuals performed novel behaviors, or known behaviors in new contexts, more often than high-ranking chimpanzees (Reader & Laland, 2001). We did however see a small effect of dominance on spread of solutions (innovation) where onlookers preferentially reproduced the inventions of higher-ranking individuals. This is reminiscent of a previous study that found chimpanzees displayed biases towards copying higher ranking individuals (Kendal et al. 2015; but see Watson et al., 2018). This suggests high 'innovation' scores in our more dominant individuals may be due to an increased likelihood of others copying them rather their being more inventive than subordinates.

Overall, we documented substantial inventions in captive populations of chimpanzees, indicating they flexibly explored the SW task. Such novel solutions applied to new problems are crucial to adapting to changeable environments and are an important component of cumulative culture (Dean et al., 2014). However, the rare solutions to more complex levels were not socially transmitted, offering one explanation as to why we have seen little experimental evidence of cumulative learning in chimpanzees, although this may relate specifically to the constructional nature of the tools required at the most complex levels of our task. However, our results echo findings for wild populations where idiosyncratic inventions often fail to transmit to others in wild populations (Boesch, 1995; Nishida, Matsusaka, & McGrew, 2009). We hope future research will continue to assess the conditions under which our close living relatives prefer to rely on personal discovery rather than social learning (and vice versa) and how solution complexity interacts with the source of information selected. A gap between human and other ape species in the reliability with which, and how readily, information is exchanged between conspecifics in potentially cumulative contexts has consequences for the spread of progressive inventions as they arise in populations, as well as for cultural complexity, which could help to explain why human culture has reached heights that remain unrivalled by other apes.

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Table 1. Model comparisons reporting WAIC for the full and null ‘participant characteristics’ models. The posterior means, standard deviations and 89% HDPIs are reported for each fixed effect.

Fig 1. Schematic of four reward exits repeated on each task level (L1-L4). The centered reward could be maneuvered left and accessed via the trapdoor or ramp, or moved to the right and extracted through the pushdoor or lift

Fig 2. (1) Functional tools that could be combined (yellow tools) or unfolded (green tools). (1a) hook end that combines with (1b) the middle section long enough to reach L2 and (1c) the handle, to create an elongated tool. Combining (1a) and (1b) was required to reach L3 and adding (1c) for L4; (1d) folded tool with an un-foldable hook on one end and a cuff that had to be removed before its extension to reach L3 and L4; (1e) flat tool long enough to reach L2. (2) Non-functional tools; (2a) thick, short PVC L-shape pipe; (2b) flimsy straws; (2c) short sections of bamboo; (2d) short, black piping and (2e) flimsy and long bamboo sections

Fig 3. L3 reward being maneuvered using a combined tool

Fig 4. All instances of repeated inventions and of subsequent productions of the same tool-exit combination by others. Note: not all innovations are depicted as there are inventions that were not repeated but still spread to others; *re-inventions may be shown but not the original invention in cases where the first invention was not repeated by the original inventor. Group indicated by initials (e.g, JI and EY). Defining terms: L. Bam = Long bamboo; TnTkTn = Thin section combined with Thick section combined with Thin; TkTnHk = Thick section combined with Thin section combined with Hook; Fol = Foliage; Sht St = Short Straight section; Fold = Folded tool; Unfold = Unfolded tool, Th+Th = Thick section combined with Thin section.

Fig 5. The number of repeated inventions made at each task level. Shading indicates social group (8 groups)

Fig 6. Percentage of available rewards retrieved at each level in each successive test hour. The number of rewards available each hour was calculated by dividing the duration of the session (60 mins) by the re-baiting schedule of that session (1-5 mins)