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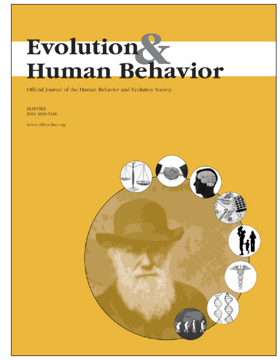


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PII: S1090-5138(16)30361-0
DOI: doi: 10.1016/j.evolhumbehav.2017.04.007
Reference: ENS 6130

To appear in:

Received date: 28 November 2016
Revised date: 17 April 2017
Accepted date: 22 April 2017

Please cite this article as: Gillian L. Vale, Sarah J. Davis, Susan P. Lambeth, Steven J. Schapiro, Andrew Whiten , Acquisition of a socially learned tool use sequence in chimpanzees: Implications for cumulative culture, (2016), doi: 10.1016/j.evolhumbehav.2017.04.007

# Acquisition of a socially learned tool use sequence in chimpanzees: Implications for cumulative culture

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Word Count: 6688

**Abstract**

Cumulative culture underpins humanity's enormous success as a species. Claims that other animals are incapable of cultural ratcheting are prevalent, but are founded on just a handful of empirical studies. Whether cumulative culture is unique to humans thus remains a controversial and understudied question that has far-reaching implications for our understanding of the evolution of this phenomenon. We investigated whether one of human's two closest living primate relatives, chimpanzees, are capable of a degree of cultural ratcheting by exposing captive populations to a novel juice extraction task. We found that groups (*N* = 3) seeded with a model trained to perform a tool modification that built upon simpler, unmodified tool use developed the seeded tool method that allowed greater juice returns than achieved by groups not exposed to a trained model (non-seeded controls; *N* = 3). One non-seeded group also discovered the behavioral sequence, either by coupling asocial and social learning or by repeated invention. This behavioral sequence was found to be beyond what an additional control sample of chimpanzees (*N* = 1 group) could discover for themselves without a competent model and lacking experience with simpler, unmodified tool behaviors. Five chimpanzees tested individually with no social information, but with experience of simple unmodified tool use, invented part, but not all, of the behavioral sequence. Our findings indicate that (i) social learning facilitated the propagation of the model-demonstrated tool modification technique, (ii) experience with simple tool behaviors may facilitate individual discovery of more complex tool manipulations, and (iii) a subset of individuals were capable of learning relatively complex behaviors either by learning asocially and socially or by repeated invention over time. That chimpanzees socially learn increasingly complex behaviors through social and asocial learning suggests that humans' extraordinary ability to do so was built on such prior foundations.

**Keywords:** Culture; Cumulative Culture; Cultural Evolution; Social Learning; Ratcheting



## 1. Introduction

Cultural technologies have evolved across generations in human societies by the gradual buildup of modifications to, and the recombination of, existing knowledge, such that (1) artifact continuity occurs between pre-existing and 'new' artifacts, and (2) artefact complexity moves beyond what an individual can invent individually in the absence of a cultural history (Basalla, 1988). This process of cumulative culture – specifically the successive addition or blending of new innovations and old, and their social spread within populations and across generations– underpins humanity's enormous success as a species and has allowed us to adapt to, inhabit, and modify (via cultural niche construction) environments we are not always biologically prepared for (Henrich, 2015; Henrich & McElreath, 2003; Odling-Smee, Laland & Feldman, 2003; Pagel, 2012; Richerson & Boyd, 2005; Tomasello, 1999). Experimental investigations with humans have begun to shed light on how cultural change occurs over time and the factors that underpin it (e.g., Caldwell & Millen, 2010a, b; Caldwell, Schillinger, Evans & Hopper, 2012; Dean et al., 2012; Derex, Godelle & Raymond, 2012; Derex Beugin, Godelle & Raymond, 2013; Zwirner & Thornton, 2015). For example, we now know that large population sizes can protect against cultural loss, enabling high levels of cultural complexity to be maintained (Derex et al., 2013), and process-copying (e.g. imitation), in many cases, can lead to superior skill acquisition than product-copying (e.g. emulation) or individual asocial learning (Derex et al., 2012; although see Caldwell et al., 2009; 2012). These studies have provided important insights into how human culture may have evolved and diversified by identifying particular learning mechanisms and social structures that promote the accumulation of increasingly complex cultural traits. Given the significance of cumulative culture to humanity, a major research question at an early stage of investigation is whether, and to what extent, other animals show any ratcheting in their cultural complexity.

The study of chimpanzees, in particular, is crucial to our understanding of the processes that have shaped contemporary humans since the time of our last common ancestor. When it comes to the evolution of culture, numerous parallels have been drawn between chimpanzees and humans (McGrew, 1992, 2004; Boesch & Tomasello, 1998; Whiten, 2011, 2017), making them an important study species in this regard. Chimpanzees, for example, like humans, display multiple-tradition cultural repertoires that vary by geographic region (Whiten & van Schaik, 2007), and complex behaviors in the wild (e.g., complex tool sets and composite tools: Boesch, 2012; Sanz & Morgan, 2007, 2009; Sanz, Schöning & Morgan, 2009) that outstrip other non-human species. Parallels have also been drawn between the social learning processes that underpin human and chimpanzee cultures. In particular, chimpanzees and humans will both engage in emulative learning, recreating cultural products from action end-products, allowing small trait modifications to occur in relatively simple tasks (Caldwell et al., 2009). Yet important species differences also exist, with humans often learning by imitating process or action information, a capability that appears more rarely or with less fidelity in chimpanzees (Whiten, McGuigan, Hopper & Marshall-Pescini, 2009). While research documenting chimpanzee cultures and the social learning processes that underpin them has exploded in recent years (reviewed in Whiten, 2017; Vale, Carr, Dean & Kendal, 2017), the question of whether chimpanzee cultures become more complex is comparatively understudied.

Our study investigated whether groups of captive chimpanzees adopt a tool modification behavior that is built upon simpler tool behavioral foundations. Documentation of the use of tool sets and composite tools in wild chimpanzees (Boesch, 2012; Sanz & Morgan, 2007, 2009; Sanz, Schoning & Morgan, 2009) is suggestive of some degree of cultural modification. Brush-tipped probes, used for termite fishing, provide one interesting case. Here, chimpanzees of the Goualougo Triangle deliberately modify herb stem probes by chewing one end to create a new tool surface that increases the tool efficiency in gathering termites, relative to unmodified tools (Sanz, Call & Morgan, 2009). Thus, we see a modification, in terms of complexity and efficiency, of an existing cultural behavior. However, investigation with captive chimpanzees concluded that cumulative learning of increasingly complex skills may be absent in chimpanzees (Dean et al., 2012; Marshall-Pescini & Whiten, 2008) or limited to small modifications in behavioral efficiency that may easily be invented by a few adept individuals (Yamamoto, Humle & Tanaka, 2013). In Dean et al. (2012) groups of capuchins, chimpanzees, and nursery school children were presented with a puzzle box containing three, increasingly difficult, task solutions. The first solution simply required participants to push open a door to reveal a low-value reward; the second solution required the depression of a button before pushing the door even further revealing a medium-value reward; and lastly, the most complex action was completed by turning a dial and pushing the door even further to reveal a high-value food reward (but note that these solutions had to occur in this sequence). Social demonstrations of the complex behavior did not greatly enhance the chimpanzees or capuchins' performances, whereas children progressed through the complex task solution. The authors concluded that the nonhuman primates of this study lacked cumulative learning, contrasting with the children who learned increasingly more complex solutions (albeit, note that this study lacked an asocial control condition and thus it is unknown whether children could have progressed through the three solutions independently). Given that the variability in the complexity of wild chimpanzee tool use and manufacture hints at a possibility of some cumulative learning, it is possible that the absence of evidence in controlled settings may be an artefact of failure to provide the right task conditions for its expression. In the wild, chimpanzees manufacture tools by detaching sticks and leaves to create tools of different lengths and diameter for specific task uses (Boesch & Boesch, 1990). Accordingly, and in contrast to previous culture studies that have required the manipulation of multiple defenses to access increasingly desirable rewards (e.g. opening doors and depressing buttons: Dean et al., 2012; Marshall-Pescini & Whiten 2008), here we presented chimpanzees with a tool modification task that required the detachment of tool material. Specifically, we examined (1) whether social learning from a model trained on a tool detachment behavior promotes the acquisition of this behavior relative to (a) groups of chimpanzees not seeded with such a model and (2) chimpanzees, tested individually, that received no social information at all (asocial controls); as well as (3) whether complex behaviors build on simpler foundations.

Previous investigation has shown that chimpanzees, provisioned with straws and a container of juice, may switch from a relatively inefficient "dip" technique to a more efficient, but readily invented, "suck" technique, either through social learning or independently through trial and error (Yamomoto et al., 2013; see also Manrique & Call, 2011 and Manrique, Gross & Call, 2010 for similar cases of apes switching from dipping behaviors to suck techniques). Building on this, we presented six groups of chimpanzees with a large juice container and multiple tools affording dipping and/or suck behaviors, with the addition that a modification of removing a stop valve attached to one end of a tube meant that it could then be used as a 'straw' – i.e. a tube for sucking juice. Removal of the stop valve required chimpanzees to turn ('unscrew') the valve. Modification and use of this tool allowed efficient juice gain relative to tools that did not require modification. As our chimpanzee population shows great difficulty in socially learning turn behaviors (Dean et al. 2012), the behavioral steps of value removal and subsequent use of the modified straw tool was considered a relatively complex behavior for our sample. Chimpanzees could alternatively use comparatively simple behaviors such as 'dipping' their hands into the juice, or using unmodified tools on the task. There were three study phases: (1) ten hours of open diffusion during which three groups were exposed to a model trained to perform this tool modification before using the tool as a straw (hereafter referred to as a behavioral sequence of 'unscrew and suck'), and three groups were not (remaining non-seeded and all group members were task naive); (2) groups subsequently received a further ten hours of task exposure but this time the three seeded groups were exposed to 10 hours of video demonstrations of the unscrew and suck behavioral sequence prior to, and during, open diffusion, while the three non-seeded groups received no such video exposure of the tool modification; (3) groups subsequently received an additional 10 hours of exposure to a modified version of the task that minimized the use of simpler tool behaviors. Phase 3 allowed an assessment of whether chimpanzees would be motivated to learn the unscrew and suck behaviors when other task solutions were unavailable to them. This is of interest given that one driver of behavioral modification is environmental fluctuation or risk, which may encourage behavioral change when past behaviors become inefficient or redundant (Buchanan, O'Brien & Collard, 2015; Collard, Buchanan & O'Brien, 2013; Collard, Kemery & Banks, 2005; Smaldino & Richerson, 2013).Behavioral change in nonhuman primates who otherwise show conservative behavior (Marshall-Pescini & Whiten, 2008) has been found to be facilitated as past behaviors become obsolete (Lehner et al., 2011; Manrique, Volter & Call, 2013) or difficult to perform (Davis et al., 2016). Again, during this phase, the three seeded groups had access to a trained model and the non-seeded groups did not. Importantly, we compared group performances to those of asocial controls that had no access to social information. This allowed testing of whether the unscrew and suck behavior could be independently learned by invention alone. This is crucial to the study of cumulative culture in which behavioral complexity must supersede what individual innovative abilities can achieve.

## 2. Method

### *2.1 Participants*

Out of the fifty-six chimpanzees (*M* age = 32.04, 36 female) who participated in this investigation, 21 chimpanzees were in the seeded condition (of which three males were trained to perform the unscrew and suck behavior); 25 chimpanzees were in the non-seeded condition; and 10 chimpanzees were in the control conditions. For the control conditions, five chimpanzees voluntarily separated from their group to participate in the task with no access to social information and five chimpanzees were exposed to phase 3 only in a group situation (phase 3 only controls; see procedure). Male demonstrators were used in this study as we could not train females on the 'unscrew' behavior despite months of positive reinforcement training and human demonstrations (see supplementary materials for further training details). Males also proved hard to train, with some not learning the unscrew behavior, or unscrewing but failing to learn the suck behavior. Despite chimpanzees finding the behavior difficult to learn in its entirety, we eventually trained three males on the complete behavioral sequence. Chimpanzees were housed at the [name deleted for review process]. The [name deleted for review process] is fully accredited by AAALAC-I. Chimpanzees were group housed with access to enriched indoor-outdoor enclosures that contained multiple climbing structures. Chimpanzee participation in this study was voluntary. Chimpanzees had prior exposure to juice-filled enrichment devices requiring sponging behaviors, and food-filled pipe feeders that required the dipping of stick tools. All chimpanzees had prior experience with receiving juice from 'wash' bottles that have a straw-like end from which juice can be squeezed or sucked out. The staff at the [name deleted for review process] squeeze juice from these bottles into chimpanzee mouths but occasionally some chimpanzees suck the juice through the straw end. Plastic bottles (that often have screw lids) not provisioned at the [name deleted for review process], and thus chimpanzee knowledge of 'unscrew' behaviors was restricted. Ethical approval was granted for this study by the [name deleted for review process] and [name deleted for review process].

Table 1. Participant rearing condition according to study condition

| | Seeded-All phases | Non-seeded-All phases | Non-seeded-Phase 3 | Asocial-Phases 1 and 3 | Models |
|---|---|---|---|---|---|
| Mother-Reared | 12 | 16 | 5 | 5 | 0 |
| Nursery-Reared | 2 | 4 | 0 | 0 | 3 |
| Wild-Born | 4 | 5 | 0 | 0 | 0 |

*2.2 Apparatus*

A single, open-topped juice container was fixed to a crate attached to a wheeled cart that was pushed flush to enclosure mesh. The juice container (37 x 27 x 28cm) was filled with diluted apple juice (4.08 liters of apple juice diluted with water until full). Five types of tool were provisioned that enabled juice retrieval by either dipping the tools, chewing the tool into a sponge, and/or using the tool as a straw (See Table 2 and Fig 1). Four tools were also retrieved by chimpanzees from their enclosure to use on the task (Table 2). The simplest method was 'dipping' the tools, as no tool modification was required before performing the behavior. Sponging, again, represented a simple tool behavior, with the added component of chewing, typically absorbent material, into round shapes, typically prior to the tool's use. Finally, four tools could be used as straws, but only two could be used without tool modification (short bamboo and short straw). The tools that served as straws without modification were short; thus, their use as straws soon depleted the juice level which rendered longer straws, that required modification for use, necessary for further juice gain. Two straws required chimpanzees to unbend them before use: the medium bendy tool and the long bendy tool. Only the long bendy tool, that also required the removal of a stop valve from one end, was long enough to efficiently retrieve all the juice from the container. The long bendy tool specifically required modification by unbending, and unscrewing a valve before use as a straw. This behavior built on more simple juice retrieval techniques, in particular using the unmodified short straws to gain juice. As the long bendy tool and long bamboo were of sufficient length to reach all the juice in the container, chimpanzees could also 'dip' these tools despite semi depletion of the juice.

Table 2. Taxonomy of tools provisioned by the experimenter or located by the chimpanzees in their enclosures, tool functions and their efficiency in gaining juice. Once chimpanzees consuming it half depleted the juice, only the long bendy tool and long bamboo could reach the remaining juice. Consumption rates were calculated by giving a single chimpanzee each tool and a container of juice. Following consistent use of the tool for one minute we calculated how much juice was depleted (ml). *tool chewed into a sponge

| Tool and description | Length (mm) | Diameter (mm) | Straw | Suck Consumption Rate (ml/min) | Dip | Dip Consumption Rate (ml/min) | Sponge | Sponge Consumption Rate (ml/min) | Provisioned |
|---|---|---|---|---|---|---|---|---|---|
| Long bendy tool with detachable valve at one end | 711.2 | 19.05 | Y | 885 | Y | 31 | N | - | Y |
| Medium length bendy tool with no valve attached | 279.4 | 12.7 | Y | 880 | Y | 28 | N | - | Y |
| Short straight tool with no valve attached | 203.2 | 5 | Y | 670 | Y | 9 | Y* | 6 | Y |
| Long thin section of leafy bamboo | 584.2 | 3 | N | - | Y | 4 | Y* | 90 | Y |
| Short section of bamboo stem with no leaves attached | 127 | 10 | Y | 621 | Y | 6 | N | - | Y |
| Kraft brown paper | Variable | NA | N | - | N | - | Y | 252 | N |
| Wood wool excelsior bedding material | Variable | NA | N | - | N | - | Y | 35 | N |
| Paper cup | 95.2 | 68.85 | N | - | N | - | Y | 50 | N |
| Foliage/plant material | Variable | Variable | N | - | Y | Variable | Y | Variable | N |
| Hand | Variable | Variable | N | - | Y | Variable | N | - | N |

*2.3 Procedure*

*2.3.1 Phase 1: Testing the role of social learning in the acquisition the novel,* unscrew and suck *tool use behavioral sequence*

The six captive chimpanzee populations (*N* = 46 chimpanzees) were provisioned with a container of juice for five two-hour sessions or until the juice container was depleted. The five types of tool were each provisioned in triplicate. Three groups ('Seeded-All phases', *N* = 18 chimpanzees, 13 female) were each seeded with a male trained on the behavioral sequence of modifying the long bendy tool (unbend, unscrew, suck: See Supplementary Materials Video 1). At the beginning of session one, this behavioral sequence was demonstrated to the Seeded-All phases groups by the trained models, achieved by the experimenter first providing the long bendy tool to the models only. Once this demonstration was completed the remaining tools were provisioned to the group.  Three groups remained non-seeded, meaning that all individuals were task-naïve at the start of the experiment ('Non-seeded-All phases', *N* = 25, 18 female). Once the juice became half depleted, only the long bendy tool and long bamboo (Table 2) could be used to gain juice. The unbend, unscrew and suck sequence allowed high juice returns at this point (Table 2), otherwise chimpanzees could perform much less efficient, long bendy tool - or long bamboo - based dip behaviors (Table 3).

Table 3. Descriptors of chimpanzees' tool behaviors

| Behavior | Description |
|---|---|
| Dip | Tool inserted into the juice before placing in mouth |
| Sponge | Absorbent or chewed up material/tool is inserted into the juice before placing in mouth |
| Fish | Tool used to retrieve a second tool from the juice |
| Combine | Tool inserted into the end of another tool |
| Suck | Hollow tool is used to suck juice from the container |
| Unbend | Straightening/unbending of tool |
| Unscrew | Removal of stop valve by twisting valve off spiral thread of the long bendy tool |

[Insert Fig 1 around here]

*2.3.2 Phase 2: Amplifying the amount of social information available*

In wild chimpanzee populations, complex behavioral sequences can take years of practice and social observation before their mastery (Matsuzawa et al., 2001; Lonsdorf, 2005). In phase two, we increased the opportunity for social observation and practice in seeded groups by playing video demonstrations of their model performing the unbend, unscrew and suck behaviors on loop for 10 hours (ca. 1200 demonstrations played) to seeded groups, both before and during task exposure. Non-seeded groups were exposed to 10 hours of a video still of a male conspecific in close proximity to the juice container prior to, and during, task exposure. Juice was again provisioned for up to 10 hours or until 5 containers of juice were depleted.

*2.3.3 Phase 3: Ecological change making LBT use yet more valuable*

In Phase 3, we introduced covered juice containers with only two small openings on top, into which the long bendy tool could be inserted. The two covered juice containers were fixed to the crate attached to the cart, and again filled with diluted apple juice. Phase 3 test sessions lasted one hour or until both containers were depleted, with 10 sessions conducted with each group. The covered containers minimized the opportunity for sponging, as the small openings made sponge retrieval difficult. Only long bendy tools were provisioned, so it became necessary for chimpanzees to unbend these tools and unscrew the valve, from the outset, to gain a substantial quantity of juice. Otherwise, subjects could perform the extremely inefficient behavior of dipping the long bendy tool into the juice.

### *2.3.4 Control Conditions*

Two attributes are fundamental to cumulative culture; (1) modification to existing traits must occur, and (2) modification must go beyond what individuals can invent for themselves. To determine whether our unscrew and suck behavior built on more simple tool use behaviors (attribute (1)) we exposed one naïve group of chimpanzees to 30 hours of the covered containers and the long bendy tools only (‘Phase 3-only controls’). This group had no prior experience with the other, simple, tools presented in Phases 1 and 2. We exposed 5 different chimpanzees to an ‘Asocial-Phases 1 and 3’ condition, in which subjects were each separately exposed to the open juice container and the five tools for 1 hour (2, 30-minute sessions; phase 1) before exposure to the covered containers and long bendy tool for an additional hour (2, 30-minute sessions; phase 3 controls; collective total test time of 10 hours; note that these asocial controls had sole access to the task during testing as they did not have to compete for access with conspecifics). During the ‘Asocial Phase 1’ control, juice was slightly depleted relative to group provisioning, so long tools would be needed sooner. At the start of the test, the juice could still be reached with sponges and the short straw to allow a potential build up in tool complexity.

### *2.3.5 Procedure: All phases*

Tools were replaced by the experimenter upon chimpanzees transporting them away from the task. This was achieved using surplus tools that could be provisioned to the chimpanzees upon tools being carried away. This meant that triplicates of each tool were usually available at the task, however extra tools were sometimes available when chimpanzees brought tools back to the task area (maximum of five tools).  Tools that were dropped outside the chimpanzees’ enclosure, including those dropped into the juice container that could not be retrieved by the chimpanzees, were pushed back through the enclosure mesh by the experimenter. Tools were always provisioned close to the juice container, well with 1m distance to the task. During periods of inactivity, modified tools left in the juice container were removed by the experimenter and returned to the chimpanzees in their original tool state (e.g. valves were replaced and the tool was folded again). This was to encourage multiple demonstrations of tool modifications and to prevent groups from simply re-using one functional tool left by the model. Behaviors were coded as occurring when a new behavior – one different to the behavior previously performed by the subject - was employed. When chimpanzees ceased performing a given behavior for more than 10 seconds before resuming the behavior, the resumption was coded as a separate behavioral instance. Attendance was also documented when individuals were within 1m with their head orientated to a conspecific using a tool. Examples of each behavior were coded by second researcher and inter-rater reliability was good (Kappa = 0.74, $N = 30$, $p < 0.001$).

## 3. Results and Discussion

*3.1 Phase 1. Testing the role of social learning in the acquisition of the novel, unscrew and suck tool use behavioral sequence*

Chimpanzees developed five different task-oriented behaviors: dipping, sponging, fishing, combining and sucking (Table 3). Individuals in the seeded groups performed proportionally more successful suck behaviors using straw tools than was observed in the non-seeded groups (Table 4). Indeed, one non-seeded group (group 2) failed to perform any suck behaviors, failing to discover that some tools functioned as straws. Chimpanzees in the seeded groups, specifically, used the long bendy tool proportionally more as a straw to gain juice (*MD* = 0 .84) than individuals in the non-seeded condition (number of successful uses of the long bendy tool as a straw/number of successful suck behaviors using any straw tool: *MD* = 0.00; Mann-Whitney U test = 85.50, *N* = 43 $p < 0.001$). Thus, exposure to a model trained to use the long bendy tool facilitated other group members' success with this particular tool. The unbend behavior, required for the use of the long bendy tool and medium bendy tool, was readily discovered by individuals in both the seeded and non-seeded groups (26 of 43 chimpanzees performed the unbend action, 14 in the non-seeded condition). As unbend was readily discovered, we do not include it as part of the long bendy tool modification in subsequent analyses.

Seven individuals (BK, TK, MA, MY, CA, ZE, HD, from Seeded groups 1, 2, and 3) successfully acquired the unscrew-valve behavior to create a functional long bendy tool that could be used as a straw to efficiently gain juice. Only one of these chimpanzees did not use her own modified tool to gain juice following the unscrew action, but she did gain juice using a tool modified by the model. Overall, 12 individuals subsequently used a modified long bendy tool as a straw to retrieve juice and all 18 of the chimpanzees in the seeded groups at least attempted to use this tool as a straw. Only four of these chimpanzees attempted to suck through the long bendy tool without first attempting to gain juice using other methods and tools. Thus, 14 chimpanzees first performed simpler methods such as dipping and sponging with tools, or sucking through unmodified short tools, before advancing to attempt or use the relatively more complex technique (note that chimpanzees had prior experience with juice squeezed out of 'wash' bottles through a straw like end). Two individuals (NI, TA, both in Non-Seeded group 1) independently discovered the unscrew-valve behavior; however, both failed to use their tool as a straw. The difference in the number of unscrew actions performed by seeded and non-seeded individuals was significant (Mann-Whitney U Test = 153.0, *N* = 43, *p* = 0.01), with 6 seeded individuals unscrewing a total of 23 valves, compared to only 3 being unscrewed by 2 individuals in the non-seeded condition (Fig 2). Overall, following valve removal by either the model or subsequent group members, the 12 individuals in the seeded condition gained juice using the long bendy tool on a total of 93 occasions whereas no individual in the non-seeded condition ever did so. This suggests that, in the absence of a trained model, rare individuals in the non-seeded condition invented part, but not the entirety, of the behavioral sequence.

Table 4. Successful behaviors used by chimpanzees according to model condition and study phase. Medians based on the proportion of behaviors used by individuals. Mann-Whitey U test statistics and *p*-values are provided comparing the proportion of behaviors employed between seeded and non-seeded groups.

| Behaviour | Phase | Median (seeded) | Count (seeded) | Median (non-seeded) | Count (non-seeded) | U | P-Value | Bonferroni corrected Alpha |
|---|---|---|---|---|---|---|---|---|
| **Dip** | **1** | **0.15** | **55** | **0.48** | **200** | **97.50** | **0.003** | 0.01 |
| Sponge | 1 | 0.23 | 93 | 0.30 | 184 | 200.00 | 0.86 | 0.01 |
| Fish | 1 | 0.00 | 5 | 0.00 | 3 | 177.00 | 0.251 | 0.01 |
| Combine | 1 | 0.00 | 9 | 0.00 | 2 | 175.00 | 0.194 | 0.01 |
| **Suck** | **1** | **0.40** | **128** | **0.00** | **115** | **96.50** | **0.002** | 0.01 |
| Dip | 2 | 0.25 | 77 | 0.11 | 68 | 144.50 | 0.204 | 0.01 |
| Sponge | 2 | 0.11 | 53 | 0.68 | 183 | 122.50 | 0.055 | 0.01 |
| Fish | 2 | 0.00 | 1 | 0.00 | 2 | 181.50 | 0.862 | 0.01 |
| Combine | 2 | 0.00 | 5 | 0.00 | 0 | 157.50 | 0.089 | 0.01 |
| **Suck** | **2** | **0.64** | **180** | **0.00** | **65** | **81.50** | **0.001** | 0.01 |
| Dip | 3 | 0.23 | 146 | 0.47 | 63 | 103.50 | 0.024 | 0.02 |
| Sponge | 3 | 0.00 | 9 | 0.00 | 16 | 140.00 | 0.173 | 0.02 |
| **Suck** | **3** | **0.75** | **428** | **0.00** | **63** | **50.50** | **<0.001** | 0.02 |

### *3.1.2 Phase 2: Amplifying the amount of social information available*

Seeded and non-seeded individuals again differed in the proportion of the suck behavior that was used to gain juice (see Table 4), and again one whole group (Non-seeded group 2) failed to discover that some tools functioned as straws. Individuals in the seeded condition used the long bendy tool as a straw proportionally more (*MD* = 1.00) than individuals in the non-seeded groups (*MD* = 0.00; Mann-Whitney U Test = 59.50, $N = 43$, $p < 0.001$, Bonferroni correction applied with alphas set at 0.02). Sixteen valves were unscrewed by seeded groups (4 individuals: ZE, TSA, HD [Seeded group 2 ] and TK [Seeded group 3]) compared to only two by a non-seeded group (group 1), again performed by the same individuals as in Phase 1 (NI and TA) (Fig 2). All of these individuals, except one female (TSA, Seeded group 2), had successfully removed a valve in Phase 1. The functional long bendy tools modified by in our Non-Seeded group 1 were not used as straws by the tool manufacturers; however, the tool left by a female chimpanzee (TA) was subsequently used to suck juice by two groupmates (BN and CE,CE doing so after watching BN get juice with this tool). Thus, for the first time, one of our non-seeded groups received demonstrations that this tool, with the valve removed, will function as a straw. In the seeded groups, two chimpanzees (TK and TSA) subsequently gained juice using the modified tool; one female (ZE) attempted to, but was unsuccessful in fully inserting her tool into the juice; and one male (HD) did not attempt to use the tool he modified on the task. Both chimpanzees that did not use their own modified tools to gain juice did so using a tool modified by their model. One individual (WI, Non-seeded group 3) discovered an efficient suck behavior by simultaneously sucking through two short straws to gain juice, doubling the amount she could gain, at least until the level dropped to where only the long bendy tool could deliver juice; a novel behavior that did not spread to others. Overall, witnessing video demonstrations of the unscrew and suck behavioral sequence did not facilitate the further diffusion of this behavior in our seeded groups as compared to Phase 1. This is in line with the finding that chimpanzees, when presented with a complex task, are more successful in learning from a live chimpanzee model than from video demonstrations (Hopper, Lambeth, Schapiro & Whiten, 2015).

### *3.1.3 Phase 3: Ecological change making LBT use yet more valuable*

The proportion of suck behaviors recorded differed according to model condition, with individuals in the seeded condition again performing proportionally more successful uses of the long bendy tool (Table 4). Six individuals (TK, BE [Seeded group 3], BK [Seeded group 1], and MA, TSA and HD [Seeded group 2]) performed the unscrew behavior, manufacturing 25 functional long bendy tools (Fig 2). One individual (BE) was new to performing the unscrew behavior, displaying it after witnessing both live and video demonstrations. In the Non-seeded group 1, the same individuals (NI and TA) that manufactured functional long bendy tools in phases 1 and 2 did so again, with the addition that another male (BN) also produced this behavior. Between these individuals, 11 functional straws were manufactured by unscrewing valves. This male (BN), new to this unscrew behavior, performed it after witnessing the now experienced male (NI) demonstrate the behavior three times. During phase 3, our original tool innovators (NI and TA) finally gained juice for the first time using the long bendy tool with the valve removed (see Fig 2). The identity of who modified the tool used by our female (TA) to gain juice is unknown as it was transported to the task area already modified. In contrast, our male (NI) was observed unscrewing the valve before subsequently using the modified tool to gain juice. Both these individuals (NI and TA) used the long bendy tool as a straw following the observation of groupmates' performing this behavior (attempted/successful). The male new to the unscrew behavior (BN) also used the long bendy tool he modified as a straw. Prior to this, in Phase 2, he had used a long bendy tool with the valve removed by his group mates.

[Insert Fig 2 around here]

### *3.1.4 All Phases*

Overall (phases collapsed), individuals in the seeded condition removed significantly more valves (64 valves removed by 9 individuals, *MD* = 0.50) using the unscrew behavior than individuals in the non-seeded condition (16 valve removals by 3 individuals, *MD* = 0.00; Mann-Whitney U Test = 139.50, *N* = 43, *p* = 0.008, Fig 2). Moreover, whereas the unscrew behavior diffused in all three of the seeded groups, it was discovered in only one of the non-seeded groups. Individuals in the seeded condition also performed significantly more unscrew *attempts* (96 attempts made by 15 individuals from all 3 groups, *MD* = 3.00) than individuals in the non-seeded condition, who made a total of only 9 attempts (performed by 2 individuals in the Non-seeded group 1, *MD* = 0.00; Mann-Whitney U Test = 54.00, *N* = 43, $p < 0.001$). Thus, exposure to a model trained to unscrew a valve before using the modified long bendy tool as a straw, facilitated valve manipulations, as well as success in its removal. Overall, significantly more individuals in the seeded condition (9 of 18) performed the unscrew action than in the non-seeded condition (3 of 25; $\chi^2(1)=7.51$, $p = 0.006$). Similarly, significantly more individuals in the seeded groups performed the whole unscrew and suck behavioral sequence (9 of 18) than occurred in the non-seeded groups (2 of 25; FET: $N= 43$, $p = 0.004$, Fig 2). Of those that performed the unscrew behavior during the course of the experiment, seven were mother-reared, three were wild-born and three were nursery-reared (note that the number of individuals includes a female in our asocial control condition [see below]). Interestingly, in addition to the seeded tool modification method, we also documented the emergence of the four modes of tool making documented in wild chimpanzee populations; namely detach, reduce, reshape and combine, and emergence of three of the five tool associative technologies that have been identified; specifically, sequential tool use, composite tool use and meta-tool examples (Table 5 based on McGrew 2013). Thus, in addition to learning the seeded unscrew tool modification (a form of detach), our chimpanzees displayed multiple methods of tool manufacture and associative technologies that mimic the methods employed in wild populations (see McGrew 2013). Thus, our captive populations, much like what has been documented in other captive populations (Hopper et al., 2014), were capable of re-inventing means in which their wild counterparts make and use tools.

Table 5. Modes of tool making and associative technologies present in the study chimpanzee population compared with examples documented in wild chimpanzees (adapted from McGrew 2013). Bold indicates that examples were seeded by our trained models.

| | **Modes of Tool Making** | | | |
|---|---|---|---|---|
| | **Detach** | **Reduce** | **Reshape** | **Combine** |
| Cases documented (captive population) | Detach a handful or more of woodwool from bedding source | Leaf removal | **Unbend** | Tool inserted into tool |
| | Detach a handful or more of paper | Shorten tool length (e.g. bite off part of straw or bamboo) | Chew or shape tool into sponge | Add valve to long bendy tool |
| | Detach foliage/plant material from source | Remove sections from detached woodwool or paper tool | | Add valve to valve |
| | | **Valve removal** | | |
| Wild examples (McGrew, 2013) | Create tool by detachment a segment from its source e.g. Leaf removed or sapling removal | Remove sections from a detached tool e.g. remove leaves from a twig) | Alter the shape of a tool e.g. the folding of leaves to create a drinking vessel | Combine multiple elements e.g. create sponge by crushing leaves together |
| | **Modes of Associative Technology** | | | |

| | Tool Set | Composite | Metatool | Secondary tool use | Sequential tool use |
|---|---|---|---|---|---|
| Cases documented (captive population) | Not required | Pull container and hold straw down flush against the juice container concurrently to gain otherwise out of reach juice | Tool inserted into a tool (combine) | Not required | Raking - one tool used to obtain another, out-of-reach, tool |
| | | | Two straws used simultaneously | | Fish - one tool used to fish another tool out of the juice |
| Wild examples (McGrew, 2013) | Multiple tools used in a set, obligatory, order e.g. sequential use of different tools used to dip for honey | The concurrent, and co-dependent, use of two tools e.g. perching on a branch while dipping with a probe tool | Two tools used as a single compound tool e.g. stones used to stabilse an anvil while nut cracking with a hammer | A tool to manufacture a tool (examples absent) | One tool used to acquire another (examples absent) |

*3.2 Do complex behaviors build on more simple foundations and can chimpanzees learn the unscrew and suck behavioral sequence in the absence of any social information?*

To investigate whether the practice of simple behaviors must precede the acquisition of behaviors of a certain high complexity, we exposed an additional group, which were task naïve and non-seeded (*N* = 5, 2 female), to the covered containers filled with juice and provisioned only the long bendy tools (phase 3). Results from this 'Non-seeded-Phase 3' condition showed that in 30 hours of task exposure, no individual in this group setting succeeded in performing, or attempted to perform, the unscrew behavior that would have created a functional straw. Thus, individuals were not successful in gaining juice using the suck behavior, nor did they even attempt to use the unmodified long bendy tool as a straw. We did, however, observe both the simpler dipping (*MD* = 0.53) and sponging (*MD* = 0.47) behaviors, and four chimpanzees discovered the unbend behavior (25 unbends documented). Our results thus show that in the absence of exposure to, and use of, functional straw tools, these control chimpanzees did not discover the unscrew and suck sequence. This compares to the Non-seeded group 1 in which use of the short straw or short bamboo tools preceded the further innovation and adoption of the unscrew and suck behavior with the long bendy tool. This implies that the observation and/or practice of simple straw use behaviors could have been important for the gradual task progression observed in the non-seeded condition (group 1). However, it is noteworthy that our 'Non-seeded-Phase 3' control consisted of only five chimpanzees. Future research should include larger sample sizes in controls designed to examine whether complex behaviors can be invented/learned without prior knowledge of simpler, related, behaviors.

To assess whether the unscrew and suck behavioral sequence performed by a model is beyond what individuals can learn asocially (i.e., in the absence of social information), we exposed five additional task-naive chimpanzees (2 female) to the same task and tools provisioned to chimpanzee groups. Thus, these five chimpanzees, unlike the 'Non-seeded-Phase 3' controls, had access to tools that required modification for their efficient use as well as those that did not, allowing a potential build-up of methods. All chimpanzees voluntarily separated for these sessions before being re-introduced to their groups. All five asocial control chimpanzees displayed dipping behaviors; four displayed sponging and three individuals used the short bamboo or short straw, when provisioned, to gain juice using the suck behavior. It is noteworthy, that two of our five asocial controls failed to gain juice using straws. This, coupled with a failure to discover the straw function of the provisioned tools documented in the Non-seeded group 2, indicates that the suck behavior was not always easily discovered. One female (SY) unscrewed a single valve in her second session before discarding the long bendy tool, mimicking what originally occurred in the Non-seeded group 1. This female did not however, repeat the unscrew behavior in sessions 3 or 4 and she never attempted to use the long bendy tool as a straw. Thus, in the absence of social information, none of these asocial controls discovered the full unscrew and suck sequence. It is possible that this behavioral sequence is within a chimpanzee's capability to invent given greater task exposure. However, testing what an individual can invent in their lifetime is generally difficult to assess experimentally given the time investment such an endeavor would require. Closer inspection of the types of tool manipulations according to task type showed that chimpanzees, when presented with the covered containers, tended to dip their finger into the juice or use the inefficient sponge behavior rather than to use the long bendy tool (see Fig 3, note that only the long bendy tool was provisioned with the covered juice containers; however, sponge material could be found in the chimpanzees' enclosures). Furthermore, the average (mean) number of task orientated behaviors performed by the asocial controls and a non-seeded group containing the equivalent number of participating chimpanzees (*N* = 5) were very similar (Phase $1_{\text{Asocial}}$ = 20.2, Phase $1_{\text{Non-seeded}}$ = 19.8; Phase $3_{\text{Asocial}}$ = 25.2, Phase $3_{\text{Non-seeded}}$ = 14).

[Insert Fig 3 around here]

Overall, our results suggest that (1) exposure to model demonstrations of tool behaviors promoted diffusion of the technique among conspecifics, with more chimpanzees in the seeded groups learning the unscrew and suck behavior than chimpanzees in non-seeded groups; (2) experience with simple tool behaviors may have facilitated the acquisition of the unscrew and suck sequence as indicated by the failure of 5 chimpanzees that lacked such experience to learn the tool modification technique in 30 hours of task exposure; (3) a complete absence of social information prevented the discovery of the full unscrew and suck behavioral sequence, at least in our small sample of 5 asocial controls, either via failure to discover the tool modification process or failure to recognize the straw function of the long bendy tool (over 10 hours of collective subject test time); and (4) in the presence of social information a subset of chimpanzees were capable of learning the full behavioral sequence despite the absence of a trained model, either through repeated invention or through the combination of invention and social learning. .

Our findings show, through controlled experiments, that chimpanzees are capable of socially learning a relatively complex behavior that appears to build upon more simple ones, in a technological example. Our results contrast with earlier studies in which exposure to model demonstrations of behavioral sequences, that built upon more simple behaviors, did not promote diffusion of the technique among chimpanzees (Dean et al., 2012; Marshall-Pescini & Whiten, 2008). As some individuals in one of the non-seeded groups eventually discovered the full behavior, we cannot be sure that discovering it is outside the innovation capabilities of at least some chimpanzees (referred to by Tennie, Call & Tomasello, 2009 as their 'zone of latent solutions'). This is important given that cumulative culture requires socially propagated behaviors to be beyond what an individual can individually invent in their lifetime. However, our findings suggest that social information facilitated the emergence of the unscrew and suck behaviors. In particular, as an alternative to independent invention, social learning across individuals in the non-seeded condition could have led to the combining of parts of the behavioral sequence in a single individual (information pooling across individuals). It is also of note that asocial control individuals appeared to show little interest in the long bendy tool that required the modification, instead relying upon the simple and inefficient methods of dipping their finger into the juice or sponging, making further invention relating to the long bendy tool appear unlikely if they had longer task exposure.

In the non-seeded groups, despite 20 hours of testing, only two individuals discovered the <u>unscrew</u> action but failed to use their potentially functional straws to retrieve juice. Rather, another two individuals (BN and CE), proceeded to use their functional straws to retrieve juice, but failed to <u>unscrew</u> a valve themselves (Phase 2). What was then of particular interest was, in Phase 3, one male (BN) closely observed a now experienced male <u>unscrew</u> three valves before then doing so himself, combining the new <u>unscrew</u> element with his earlier discovered <u>suck</u> behavior. Moreover, the male experienced in <u>unscrewing</u> valves did the converse, observing others successfully gain juice using a modified long bendy tool prior to performing the full complex behavior (Fig 4). That the <u>unscrew</u> and <u>suck</u> behavior emerged after individuals watched others display the components they lacked but then went on to perform, presents circumstantial evidence that social learning was involved, especially against the background of our more robust results from the controlled experimental contrasts, demonstrating the strong effect of observational learning available to the seeded but not the non-seeded and asocial groups. However, we acknowledge that the full behavior could have been invented in the non-seeded group. Further research should address whether model demonstrated behaviors are socially transmitted that are not within individual chimpanzees' capability to invent in part or in their entirety, in the absence of social demonstrations.

[Insert Fig 4 around here]

We need to address the possibility that the longer task exposure, and/or the ecological pressure introduced in Phase 3, may have been responsible for these achievements rather than observational learning. Previous research has found that orangutans and chimpanzees are more likely to flexibly modify their behavior when known behaviors become ineffective (Lehner et al., 2011; Manrique et al.,

2013) or difficult to perform (Davis et al., 2016). Accordingly, long bendy tool use may have been facilitated in Phase 3 as past, suboptimal behaviors became obsolete or more difficult to perform with this simulation of such an ecological change. Thus, recognition that the modified long bendy tool, with the valve detached, functioned as a straw could have occurred by (1) receiving social demonstration of the behavior by BN in Phase 2; (2) longer task exposure, practice and social facilitation that arises from being in the presence of conspecifics, or (3) an increase in motivation and need to use the long bendy tool as a straw due to the removal of simpler tools in this phase. If these effects were indeed the results of social learning, we would have evidence that chimpanzees were capable learning a relatively complex behavior that has not been shown before. Such effects may mirror, in a small way, the demands of niche-change and social learning in the rise in importance of culture in human evolution.

In conclusion, and consistent with some observations from the field (Sanz et al., 2009; Boesch 2012), our findings suggest that our closest living relatives possess a greater capacity for socially learning increasingly complex behaviors than is often assumed. Our findings show that chimpanzees can socially learn a relatively complex behavior through social learning (seeded groups), and by progressive asocial learning or pooling information across individuals (the combination of asocial and social learning [non-seeded group 1]), suggesting that humans' extraordinary ability to do so was built on such prior foundations. Such abilities in our common ancestors would have provided some minimal, but important, foundations for the cumulative capacity that later underwrote human evolution and the global success of our species (Henrich, 2015; Henrich & McElreath, 2003; Pagel, 2012; Richerson & Boyd, 2005; Tomasello, 1999). Future research should further increase task complexity to explore whether chimpanzees acquire behaviors that can only be learned socially.

**Acknowledgments**

We thank all the staff at the [name removed for the review process]. We especially thank [names removed for the review process] for their aid in training our models to perform the complex behavior, and [name removed for the review process] for her comments on an earlier version of the manuscript.

**Data Availability**

The data associated with this research are available at [link].

**Funding**

This work was supported by the [names and grants removed for the review process].

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Fig 1. Tools provisioned in their original-unmodified state. From top to bottom: short bamboo, short straw, medium bendy tool, long bamboo and long bendy tool.

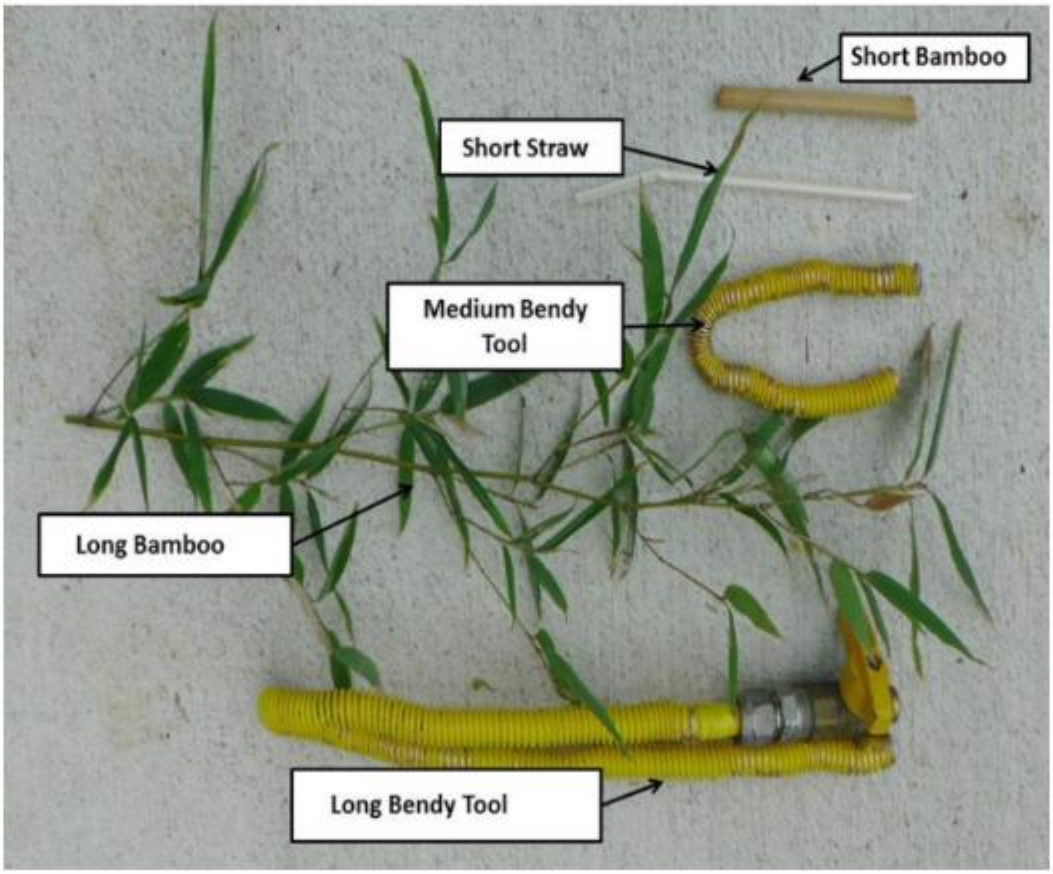

Fig 2. (a) Number of valve unscrews according to model condition and study phase; (2) Number of individuals that unscrewed a valve and successfully gained juice using a long bendy tool, made by any individual, according to model condition and study phase; (c) Number of individuals that performed the whole complex behavioral sequence by unscrewing and using their own modified tool to successfully gain juice; (d) Number of individuals that used a long bendy tool with a valve removed to successfully gain juice, according to model condition and study phase. Seeded *N* = 18 and Non-seeded *N* = 25 chimpanzees. Note: 9 and 3 individuals account for the unscrew actions made in the seeded, and non-seeded, condition respectively.

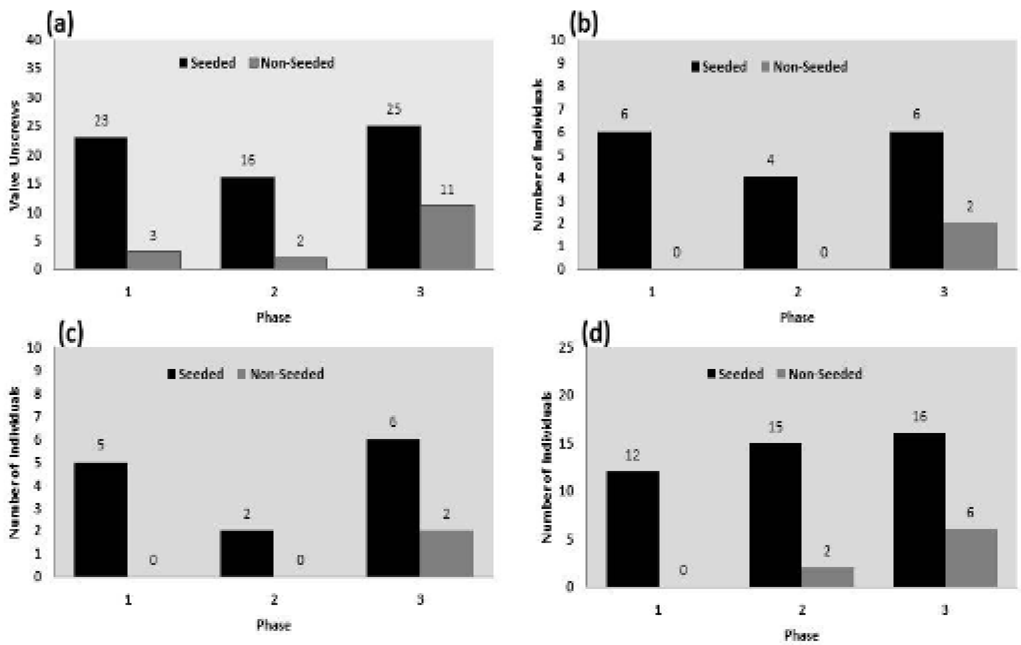

Fig 3. Behaviors used to gain juice by asocial control individuals according to the tool used and task type (open juice container/covered juice container). Only the tool methods/behaviors available in both tasks and defined in Table 2 are reported. Note: 'Hand' in the covered juice container refers to dipping of the finger into the small container openings.

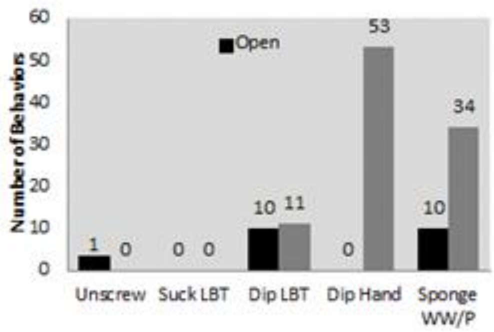

Fig 4. Discovery of the unscrew and suck behavior in the Non-seeded group 1.