

# Captive great apes tend to innovate simple tool behaviors quickly

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## Abstract

Recent studies have highlighted the important role that individual learning mechanisms and different forms of enhancement play in the acquisition of novel behaviors by naïve individuals. A considerable subset of these studies has focused on tool innovation by our closest living relatives, the great apes, to better understand the evolution of technology in our own lineage. To be able to isolate the role that individual learning plays in great ape tool innovation, researchers usually employ what are known as baseline tests. Although these baselines are commonly used in behavioral studies in captivity, the length of these tests in terms of number of trials and duration remains unstandardized across studies. To address this methodological issue, we conducted a literature review of great ape tool innovation studies conducted in zoological institutions and compiled various methodological data including the timing of innovation. Our literature review revealed an early innovation tendency in great apes, which was particularly pronounced when simple forms of tool use were investigated. In the majority of experiments where tool innovation took place, this occurred within the first trial and/or the first hour of testing. We discuss different possible sources of variation in the latency to innovate such as testing setup, species and task. We hope that our literature review helps researchers design more data-informed, resource-efficient experiments on tool innovation in our closest living relatives.

## KEYWORDS

baseline tests, captive settings, great apes, innovation, tool use

## 1 | INTRODUCTION

The acquisition of behaviors by animals is arguably mediated by a complex combination of genetic predispositions, social learning mechanisms, individual learning mechanisms, and environmental factors (Bandini, Motes-Rodrigo, et al., 2020; Laland & Galef, 2009). Among behavioral domains, technology has been a recurrent focus of

ethological studies (Sanz et al., 2013; Shumaker et al., 2011). Tool use is often investigated as a proxy of physical cognition and mental reasoning—both in human (Reindl et al., 2016) and non-human animals (henceforth animals, Taylor et al., 2007). Primate tool behavior (specifically non-human great ape behavior) is also investigated from a comparative perspective to better understand the emergence and evolution of human technological proficiency (Arroyo et al., 2016;

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Boesch et al., 2017; Marchant & McGrew, 2005; Pascual-Garrido, 2018; Toth et al., 1993).

A subset of studies in this subfield of primatology focus on tool innovation and on whether social demonstrations play a role in the acquisition of tool behavioral forms (henceforth tool behaviors) by naïve individuals. It is sometimes assumed in the primate cognition literature that, due to their inherent complexity (Shettleworth, 2010), primate tool behaviors are mainly learned by observing others modeling the behavior (i.e., via copying social learning; Boesch et al., 2020; Whiten et al., 2001). However, this assumption has been repeatedly questioned over the years (Byrne, 2007; Galef, 1992; Tennie et al., 2009) by reappraising the role that noncopying social learning mechanisms, such as different types of enhancement (Fragaszy et al., 2013) and individual learning (Motes-Rodrigo & Tennie, 2021), play in the acquisition of novel tool behaviors. In recent years, more and more studies employ observational (Falótico et al., 2021; Schuppli & van Schaik, 2019; Schuppli et al., 2016) and experimental methodologies (Bandini, Motes-Rodrigo, et al., 2020; Hopper et al., 2015) aimed at disentangling the role that different learning mechanisms play in the acquisition of novel tool behaviors.

Such experimental methodologies often include two general types of experimental conditions: baseline tests and social learning conditions. During baseline tests naïve participants are provided with all necessary materials to perform a novel behavior, but no information regarding the form of the behavior (i.e., the know-how, environmental results and/or bodily actions) is provided. Baseline tests address whether individuals of a given species could spontaneously innovate a tool behavior in the absence of social demonstrations via individual learning alone. Importantly, although the mere provision of materials often inadvertently conveys certain information about the task investigated (e.g., know-what), the behavioral form cannot be conveyed in this manner. To conduct valid baseline tests, the naivety of the participants must be ensured. That is, to evaluate how a tool behavior is innovated, the behavior of interest must not be included in the individual's own or the individual's group repertoires before the start of the experiments. If a behavior is expressed during a baseline test by naïve individuals, then this would indicate that individual learning (together with enhancement) can be sufficient for its acquisition. However, positive results in a baseline test do not indicate that all individuals of a species learn the tested behavior individually but rather that this possibility exists.

If a tool behavior is not innovated during a baseline test, it is possible that the behavior might not be spontaneously learnt by naïve individuals. Given that only a limited number of individuals would have been tested (and not the entire species for obvious reasons), the confidence on this result would depend on both the specific characteristics of the subjects tested (e.g., motivation levels, previous experience) and the sample size: the higher the number of individuals tested in a baseline that do not innovate the behavior the higher the probability that spontaneous innovation is not possible. Following a negative baseline test result, individuals proceed to a series of social learning conditions in which different types of information are provided in successive stages to evaluate the nature of the information

that the animals require to innovate the tool behavior. During the initial social learning condition, the salience of a given location or stimuli type is increased, thus evaluating the magnitude of the influence of different types of enhancements on tool innovation. In successive conditions, information about the end-product, the object's movements and finally the bodily actions involved in the tool behavior are provided to test whether different types of emulation or imitation learning lead to the acquisition of the novel tool behavior (see, e.g., Bandini, Motes-Rodrigo, et al., 2020; Hopper et al., 2015). As before, positive and negative results in these social conditions inform us about the probability that the tested behavior is learnt via certain mechanisms by individuals of the species under investigation.

This step-wise methodology has been employed in primatological studies to investigate the reliance of primate species on different learning mechanisms. Baseline tests have been in use since the advent of ethology as a scientific discipline (Tinbergen, 1948) and step-wise methodologies have been previously applied to investigate different aspects of primate tool use acquisition. For example Price et al. (2009) tested chimpanzee's abilities to build and use a composite tool either individually in a baseline test or after seeing video demonstrations containing different types of information. The authors found that seeing full video demonstrations performed by a conspecific significantly improved performance in the task (although note that one individual performed the task in this form during the baseline). Hopper et al. (2015) tested chimpanzees in different experimental conditions to evaluate which was the minimal information required by the chimpanzees to learn how to operate a puzzle box that required the use of tools to obtain a food reward. The authors found that the chimpanzees only started to succeed in the task when behavioral demonstrations (by a human) were provided (Hopper et al., 2015). Marshall-Pescini and Whiten (2008) investigated nut-cracking acquisition in a group of rescued, sanctuary-living chimpanzees using both baseline and social learning conditions. The authors of the study found that one chimpanzee readily engaged in nut-cracking during the baseline and that the remaining chimpanzees started performing the behavior after seeing social demonstrations. However, other studies that applied similar step-wise methodologies did not actually find that the tested subjects acquired the novel behaviors of interest (e.g. nut-cracking), neither spontaneously nor after demonstrations had been provided (Neadle et al., 2020).

Zoological institutions like zoos, sanctuaries, and research centers, play a crucial role in the conduction of experiments investigating tool innovation such as those mentioned above. Keepers at zoological institutions often keep records of the life histories and (sometimes) past research experiences of the animals they house. These records are an invaluable source of information for cognition researchers investigating the learning mechanisms underlying behavioral acquisition because they allow to determine whether test participants are likely naïve or not to the behavior of interest. As previously mentioned, it is fundamental to ensure participant naivety before the start of certain experiments to be able to conclude that, if the novel behavior emerges in baseline tests, individual learning and some types of enhancement suffice for the acquisition of the behavioral form.

Furthermore, zoological institutions also keep detailed records of the rearing background of the individuals they house. Such information is particularly useful for innovation experiments given the research suggesting that the social learning abilities of certain primate species such as chimpanzees and orangutans can be enhanced by the prolonged exposure to a human cultural environment and specific types of training (Call, 2001; Furlong et al., 2008; Pope et al., 2018; Tomasello et al., 1993).

Zoological institutions further allow researchers to implement a variety of testing setups during tool innovation experiments. By providing the opportunity to conduct both individual and group tests, zoological institutions give researchers the possibility of manipulating the sources of information to which individuals have access during testing. Such experiments can provide important insights regarding the effect or lack thereof that being in a group setting has on innovation probability (e.g., via response facilitation; Amici et al., 2014). The stable environment that individuals inhabit in captivity also allows researchers to conduct follow up experiments on previously tested individuals and to apply comparable testing procedures across individuals and/or groups.

Experiments in zoological institutions, including tool innovation experiments, are often subject to what is known as captivity bias or the captivity effect (Haslam, 2013; Meulman et al., 2012). This bias is supported by studies reporting that captive animals (particularly primates) outperform their wild counterparts in certain tasks. Potential explanations for this bias are the increased contact between individuals due to a more limited space in captivity compared to the wild, increased free time, almost absent predatory risk, food provisioning, behavioral enrichment, and increased terrestriality in captive settings. These factors have been suggested to correlate with higher levels of curiosity and lower neophobia levels in captivity compared to the wild (Forss et al., 2015), which might lead to higher innovation rates in captivity fueled also by food provisioning during tests (Leca et al., 2010; Yamagiwa, 2010). Alternatively, precisely because apes' physiological needs are covered by caretakers, captive apes might be under less selective pressure than wild conspecifics to innovate novel behaviors, particularly in a foraging context (Grund et al., 2019). This lack of need to develop novel foraging behaviors might be reflected in lower innovations emerging in captive populations on a regular basis.

Studies in captivity that have used step-wise methodologies such as those outlined above (or parts of it), have highlighted the crucial role that individual learning can play in the acquisition of various primate and nonprimate tool behaviors (Bandini & Tennie, 2017, 2019, 2020; Bernstein-Kurtycz et al., 2020; Rutz et al., 2016). These and other studies (Motes-Rodrigo & Tennie, 2021) have revealed that while certain types of information are frequently under social influence in many animal species (namely, know-what, -where, -who, -when), acquisition of know-how via the observation of demonstrations seems to be extremely rare regardless of species, population, task, and testing setup (Clay & Tennie, 2017; Motes-Rodrigo et al., 2021; Tennie et al., 2009, 2012). Despite the importance of unraveling the roles that different learning mechanisms play in tool

behavior acquisition and the usefulness of detailing a methodology to address this question, certain details of said methodology such as the optimal testing duration, remain unstandardized and uninformed by actual data. In other words, currently there is no agreement among researchers investigating tool innovation regarding how long a behavioral baseline should be to give the apes enough time to acquire the novel behavioral form (see also Tennie et al., 2020). Different approaches can be taken on this regard.

Some researchers have proposed that baseline tests should be implemented in the long-term and expanding several years (Bandini, 2021). In an ideal scenario freed of resource-limitations, such approach would allow to account for lifelong possibilities of innovation, resembling what some species encounter in the wild to a certain degree. However, the reality is that economic and human resources are strongly restricted in most research labs and conducting such long-term baselines might be too costly in terms of observation time, data processing and testing materials. Even the helpful suggestion of using motion-triggered cameras, incurs maintenance costs in addition to the cost of the cameras themselves. Another issue of this long-term approach is that results (and ensuing debates) could be delayed in time (as acknowledged by Bandini, 2021). Whereas eventual tool innovation in a long-term baseline would be an important result, it could come years after the start of the experiment (or may not come at all). Realistically, most researchers (especially in an early career stage) working on tool innovation and learning cannot wait an undefined number of years to obtain experimental results. Furthermore, long-term baselines leave unspecified the termination point of the experiment. Although Bandini (2021) suggests some variables that should be taken into consideration when conducting long-term baselines such as the complexity of the task and the existence of a sensitive learning period, no formula exists to calculate an exact termination point. Given these concerns, although we acknowledge the potential value of long-term baselines, we believe that there is a need for a more standardized and accessible experimental approach to investigate tool innovation.

To help researchers design data-informed, resource-efficient experiments on tool innovation, we conducted a literature review of studies that tested or reported the abilities of great apes (our study species) to innovate novel tool behaviors (i.e., in the absence of social demonstrations or training). From these studies we collected data on the testing methodology employed (see below) putting special emphasis on the timing of emergence of the novel tool behaviors to assess whether there exists an "early innovation tendency" (as implied by Tennie et al., 2020). By early innovation tendency we refer to evidence stemming from different studies, tasks, species and populations showing that apes can innovate unfamiliar tool behavior within the first few trials/hours of an experiment. Thus, the goal of this literature review was to provide a descriptive analysis of the relative time and number of trials that great apes require on average to innovate different tool behavioral forms across zoological institutions and testing setups. In this review we focus on individual-level innovations as products (Carr et al., 2016; Reader & Laland, 2003). We use the definition of innovation provided by Reader and Laland

(2003) where an innovation is "a new or modified learned behavior not previously found in the population." Although we acknowledge that innovations can also be understood as processes (Reader & Laland, 2003) and that individual-level innovations can be tightly linked with cultural innovations operating at group-level (Carr et al., 2016), our focus is on the timing of initial development of innovations from a naïve state. We hope that the data resulting from this literature review can be useful to researchers in designing more cost- and time-efficient experiments investigating the learning abilities of our closest living relatives.

## 2 | MATERIALS AND METHODS

We collected data on the timing of tool innovations in great apes from three sources. The first source was the review paper by Bandini and Tennie (2020) in which the authors compiled studies that had investigated the individual learning abilities of animals ( $N_{\text{entries in data set}} = 18$ ). The second source were papers known to the authors of the present manuscript but not included in the review by Bandini and Tennie (2020) ( $N_{\text{entries}} = 5$ ). The third source was a literature search in Google Scholar using 35 search terms ( $N_{\text{entries}} = 42$ ). These terms were generated as follows: (great ape OR bonobo OR chimpanzee OR gorilla OR orangutan) AND (novel OR never seen before OR spontaneous OR individual learning OR innovation OR insight OR acquisition) AND tool use. The titles and abstracts of the first 50 results from each search term were evaluated, and all potentially relevant studies were read in detail. Innovations were considered as such regardless of whether they were the specific target of the experimental manipulation or whether they arose as one of many solutions to the task (i.e., predicted or unpredicted by the experimenters).

All studies compiled from the abovementioned three sources were checked for the following criteria: (1) the study involved great apes and at least one experimental manipulation (it was not purely observational); (2) the innovated behavior was not present in the individual's or group's repertoire before the start of the experiment (as described by the authors); (3) no demonstrations of the innovated behavior were provided before or during the experiment to the participating great apes; (4) the behavior investigated was tool-related; (5) the timing of behavioral emergence was reported in terms of trial number or time since the start of the experiment; and (6) experimental setup was reported (i.e., individual or group testing). In group tests, when a single individual in the group expressed a novel tool behavior (innovation took place) it was considered that the group as a single testing unit had innovated. However, note that this approach might be overly conservative in some cases where it is possible to determine whether group members have or have not observed a tool innovation in their group.

Some studies that investigated behavioral acquisition in great apes had to be excluded from our review because they did not fulfill one or more of the inclusion criteria. For example, the study was purely observational (criterion 1: Nakamichi, 1999), the behavioral solution was already in the subject's repertoire (criterion 2: Hopkins

et al., 2015; Nakamichi, 2004; Yamamoto et al., 2013), behavioral demonstrations were provided to the test subjects (criterion 3: Call & Tomasello, 1994; Osvath & Osvath, 2008), the behavior was not tool related (criterion 4: Call & Tomasello, 1995), the exact timing of behavioral emergence was not reported (criterion 5: Price et al., 2009; Toth et al., 1993; Whiten, 2005; Yamamoto et al., 2013) or the experimental setup was not reported (criterion 6: Gruber, 2016; Price et al., 2009).

From those studies that fulfilled the abovementioned criteria, the following variables were collected: (1) study reference; (2) species tested; (3) number of independent testing units included in the study (if one group of apes was tested the number of independent testing units was one); (4) number of innovating units; (5) experimental setup (group or individual testing); (6) tool behavior tested; (7) tool-type (based on the classification by Shumaker et al., 2011); (8) whether the behavior tested involved tool making, tool use or both; (9) tool material; (10) action-type (based on the modes described by Shumaker et al., 2011); (11) number of trials until first innovation; (12) time until first innovation; (13) total number of trials implemented per testing unit (if different testing units were tested in different number of trials, the average is reported); (14) total testing time; and (15) tested population. If individuals from different institutions were included in the same study, each institution constituted a different entry in the data set. Given our working definition of tool innovation as a product (Reader & Laland, 2003), if a study tested or reported the use of different tools in the same task and the subjects innovated the use of different tools, each tool innovation was recorded separately in the data set (e.g., Harrison & Whiten, 2018; Kitahara-Frisch & Norikoshi, 1982; Lehner et al., 2011).

All data was processed in R version 3.6.1 (2019-07-05). No statistical tests were conducted in this study as it was not possible to evaluate the effect that the specific tool behavior investigated had in the probability of behavioral acquisition or the time until acquisition. The research presented here complied with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates. Given that no data was collected for this project, no specific ethical approval was required for its conduction. All data and code used in this manuscript can be found in the OSF project [https://osf.io/p7r68/?view\\_only=9137d23f65374ea3b23fc5f0da4cb8d8](https://osf.io/p7r68/?view_only=9137d23f65374ea3b23fc5f0da4cb8d8) (Motes-Rodrigo & Tennie, 2021).

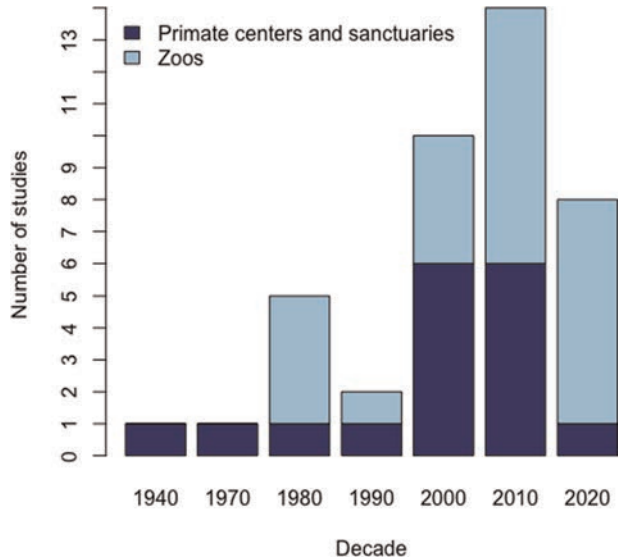
## 3 | RESULTS

Our literature search yielded 68 different tool innovation experiments from 39 different papers spanning from 1945 to 2021. Thirteen of the experiments did not result in tool innovation whereas all the others found tool innovation in at least one of the tested units. All experiments that found tool innovation reported the trial in which the tool behavior tested emerged for the first time whereas only 37 experiments reported the time of emergence (i.e., minutes since the start of the experiment). Most tool behaviors were tested in chimpanzees ( $N = 34$ ) and orangutans ( $N = 24$ ), whereas bonobos ( $N = 3$ )

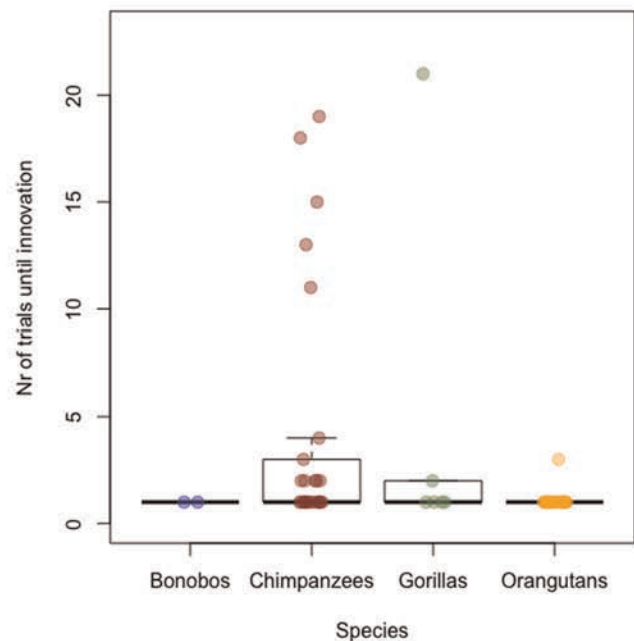
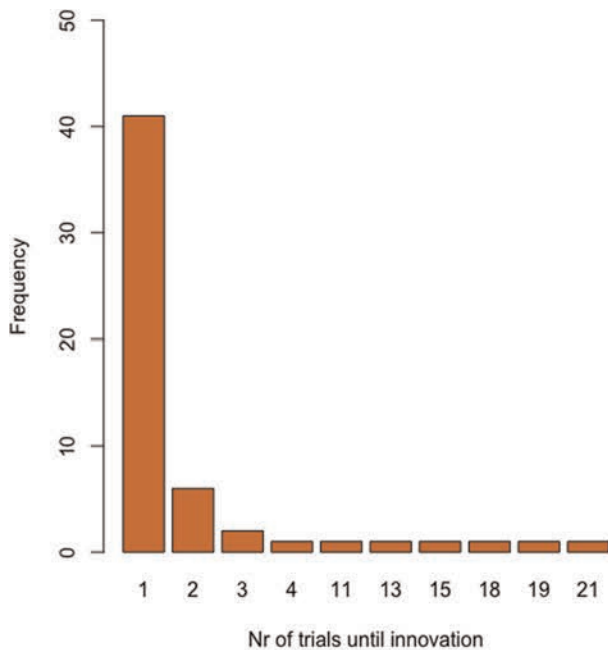
and gorillas ( $N = 7$ ) were tested much less frequently. Half of the experiments tested great apes in a group setting ( $N = 34$ ). Regarding the publication date of these studies, 80% of papers (31/39) were published after the year 2000 and 54% (21/39) were published in the last decade. The experiments included in our data set were conducted in 28 different zoological institutions. Forty of the experiments included in our data set tested great apes in zoos, 16 tested apes in primate centers (including research laboratories) and 9 tested

apes housed in sanctuaries. Some institutions hosted research activities reported in various studies included in our data set such as The Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas M.D. Anderson Cancer Center in Bastrop, Texas, USA ("Bastrop," 3) and the Wolfgang Köhler Primate Research Center in Leipzig zoo, Germany (5). The number of studies included in our data set that were conducted in zoos has overall increased over time (Figure 1) and is particularly high in the past 2 years (2020 decade), making it likely that this upward tendency continues in future.

When the number of trials until tool innovation was investigated, we found that in 75% of experiments where innovation took place (41/55), the examined tool behavior emerged in the first trial of the experiment (Figure 2). Among the experiments that reported the longest innovation latencies were Natale et al. (1988) who tested the ability of a gorilla to rake in a food reward using a tool (21 trials); Kitahara-Frisch and Norikoshi (1982) who reported the different ways in which two chimpanzees retrieved liquid from a bottle, including by producing and using brushed-ended sticks (19 trials); Tomasello et al. (1987) who tested the ability of chimpanzees to innovate the use of a rake to obtain out of reach food (18 trials) and Manrique and Call (2011) who tested the ability of chimpanzees to use a straw (15 trials). When experiments were separated according to the testing setup used, it was observed that the average number of trials required for tool behavior acquisition was slightly higher when individuals were tested individually than when tested in groups (group: mean  $\pm$  SD =  $2.58 \pm 4.11$ , range = 1–19; individual: mean  $\pm$  SD =  $3.2 \pm 5.66$ , range = 1–21), although the ranges of number of trials until innovation greatly overlapped between the two test settings illustrating a very small effect size. Regarding species



**FIGURE 1** Stacked histogram of the decades when the studies compiled in our literature review were published. Different colors represent the different types of zoological institutions where the experiments were conducted



**FIGURE 2** Left: Barplot of the reported number of trials required by great apes to first innovate a novel tool behavior. Right: Boxplot of the numbers of trials required by different ape species to innovate novel tool behaviors. Each data point corresponds to a different innovation



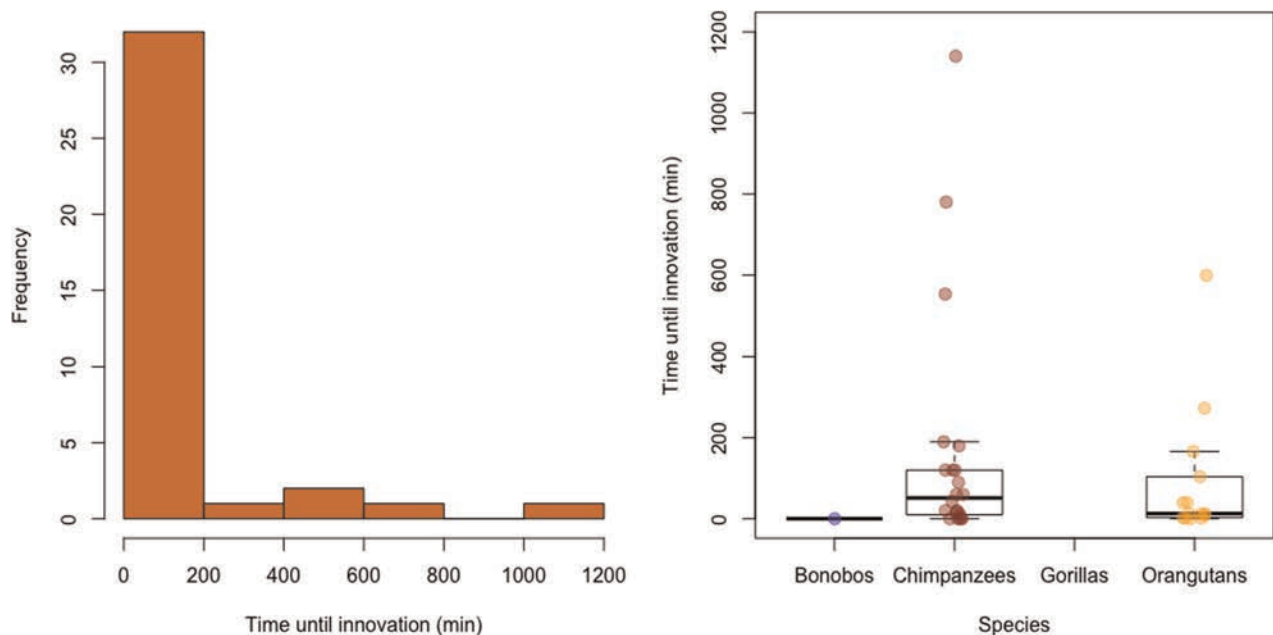
differences among experiments that reported trials until innovation, chimpanzees took an average of 4.2 trials to innovate the tool behaviors (SD = 5.80; range, 1–19;  $N = 25$ ); orangutans took 1.09 trials on average to innovate (SD = 0.42, range, 1–3;  $N = 23$ ), gorillas 4.5 trials (SD = 8.09; range, 1–21,  $N = 6$ ) and bonobos 1 trial (SD = 0.00;  $N = 2$ ).

Looking at the time required for great apes to innovate tool behaviors in experimental conditions, we found that in 65% of cases where the timing was reported or could be estimated based on trial length (24/37), great apes innovated the tool behaviors within the 1st hour of testing (Figure 3). Most of the latency data available came from studies on chimpanzees ( $N = 22$ ) and orangutans ( $N = 14$ ). We did not find any study that reported the time until innovation in gorillas and only one study that reported time until innovation in bonobos (Visalberghi et al., 1995). Chimpanzees took an average of 161 min to innovate tool behaviors and time until innovation varied broadly across studies (SD = 291, range 0.08–1140). It took orangutans an average of 91 min to innovate tool behaviors and their time until innovation also varied considerably between studies (SD = 166, range, 0.23–599). Subjects tested in a group setting were on average slower to innovate the behaviors (mean  $\pm$  SD = 206  $\pm$  298 min, range = 0.72–1140) than apes tested individually (mean  $\pm$  SD = 18.2  $\pm$  33.3 min, range = 0.08–120) although groups varied eight times more than individually tested subjects in their time until innovation.

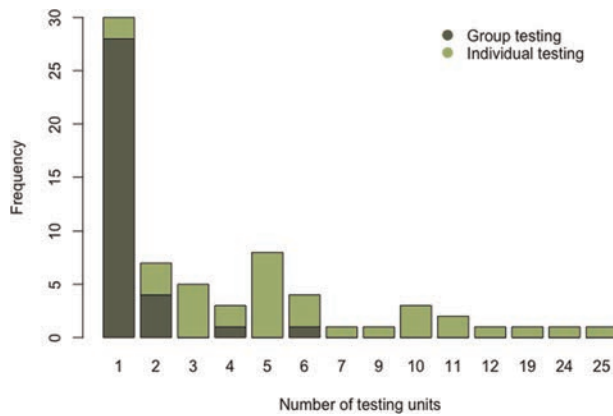
Regarding the behaviors investigated in the different experiments, in 57 cases the apes were tested on their tool using abilities whereas eleven experiments reported innovations of both tool making and tool using behaviors (e.g., Bandini et al., 2021; Boose

et al., 2013; Kitahara-Frisch & Norikoshi, 1982; Laumer et al., 2017; Lehner et al., 2011; Lonsdorf et al., 2009). Most tool behaviors investigated involved simple tool use (61/68) but in some cases more complex types of tool use were studied. For example, two studies (Neadle et al., 2020; Sumita et al., 1985) investigated the spontaneous tool innovation of nut-cracking, a composite tool behavior where a hammer and an anvil are used simultaneously to crack open an encased food. Three experiments tested apes' spontaneous abilities to innovate a secondary tool behavior where a tool is used to create another tool (Shumaker et al., 2011), namely the use of a stone hammer to detach a sharp-edged stone from a stone core that could then be used as a cutting tool to access a puzzle box (Bandini et al., 2021; Motes-Rodrigo, 2020). None of the apes tested on their abilities to innovate composite or secondary tools succeeded in the task. A single experiment tested apes' abilities to innovate a tool set involving two tools that had to be used in succession to access a food reward (Bernstein-Kurtycz et al., 2020) and found that apes could successfully learn the two-tool sequence spontaneously.

The experiments compiled in our data set reported innovations of tool behaviors involving a variety of materials. Materials such as sticks (31), water (8), leafy branches (7), wood wool (2), wood (2), paper (2), stone (4), plastic (2), a vegetable (1), and wire (1) were provided as tools directly to the apes or were used to create the tools that the apes were provided with (e.g., rakes made of wood). Water was used as a tool in eight experiments applying the floating peanut task (e.g., Hanus et al., 2011; Mendes et al., 2007). Most studies in our data set (22) reported tool innovations that involved simple actions such as probing (Boose et al., 2013; Lonsdorf et al., 2009), absorbing (8; Kitahara-Frisch & Norikoshi, 1982; Lehner et al., 2011)



**FIGURE 3** Left: Histogram of the time elapsed (in minutes) during the experiments until the first tool innovation took place. Right: Boxplot of the latencies until innovation of novel tool behaviors reported for the different ape species. Each data point corresponds to a different innovation



**FIGURE 4** Stacked barplot of the number of testing units included in the experiments compiled in our literature review. Different colors represent different testing setups

and pushing or guiding objects (9) from mazes and puzzle boxes (Bardo et al., 2017; Visalberghi et al., 1995). Some studies reported innovations where tools were used to rake in out-of-reach food (7; e.g., Natale et al., 1988; Tomasello et al., 1987). Forceful hitting actions such as pounding or hammering using tools were also occasionally tested for (7) in tasks such as nut-cracking (Needle et al., 2020; Sumita et al., 1985) and sharp stone detachment (Bandini et al., 2021; Motes-Rodrigo, 2020). Three experiments tested apes' abilities to innovate the use of straws (Manrique & Call, 2011; Morimura, 2003), one experiment tested tool excavation (Motes-Rodrigo et al., 2019) and one food scooping (Bandini & Tennie, 2017).

Regarding the sample sizes of the experiments included in our data set, we found that in 44% of cases (30/68) a single independent unit was tested. When we split the data into experiments that had tested groups or single individuals (Figure 4), we found that the median sample size of group tests was 1 whereas the median of individual tests was 5 and that the average sample size in individual tests was higher than that of group tests (group: mean  $\pm$  SD = 1.35  $\pm$  1.01, range = 1–6; individual: mean  $\pm$  SD = 6.97  $\pm$  5.64, range = 1–25). One of the studies included in the data set tested the same species both individually and in a group setting (Hopper et al., 2007). In addition, only 18% of the studies included in our data set (7/39), tested more than one species with the same methodology. Regarding test frequency, eight of the experiments only conducted one trial.

## 4 | DISCUSSION

We reviewed the timing of innovation of novel tool behaviors in captive great ape experiments in the absence of demonstrations and training. Our results show that in the majority of cases naïve individuals innovated the tool behavior in the first trial of the experiment and within the first hour of testing. Therefore, there seems to be a generalized early innovation tendency of tool behaviors in captive great apes, especially when these involve simple forms of tool

use. Our review shows that the tested great apes could quickly and with very little exploration learn novel tool behaviors, thereby indicating a strong reliance on individual learning for tool acquisition (as no demonstrations were given of the know-how underlying the behavior). Given the provision of testing materials and apparatuses in most of the experiments compiled in our data set, it is likely that several noncopying social learning mechanisms (such as local and stimulus enhancement) also contributed to the innovation of the reported tool behaviors.

This early innovation tendency observed in our review is most likely influenced by the social and ecological environments inhabited by the tested apes. Previous studies have shown that captive populations of the same species differ in curiosity measures such as exploration tendencies and neophobia (Forss et al., 2019, 2020), which in turn might influence their novelty responses and their probability of innovating a novel behavior. This within-species variation might be due to differences in social structure between groups housed in different institutions, different enrichment programs, and as we discuss below, different levels of experience in research experiments. On a bigger scale, studies comparing captive and wild apes have shown that captive apes present lower levels of neophobia and enhanced exploratory tendencies than their wild counterparts (Forss et al., 2015; see also "captivity effect") as a consequence of the large amount of "free time" that captive apes possess in their relative risk-free environments (Haslam, 2013). Therefore both the setting (wild or captive) and the specific facility inhabited by the apes are likely to influence the timing of innovation of tool behaviors.

Despite finding a general early innovation tendency, we found some outliers within our data set consisting of experiments that reported a relatively high number of trials and latency until tool innovations (Kitahara-Frisch & Norikoshi, 1982; Manrique & Call, 2011; Natale et al., 1988; Tomasello et al., 1987). In the case of Kitahara-Frisch and Norikoshi (1982) different tool behaviors employing different tool materials were innovated throughout the experiment, with the most efficient behavior being innovated last, perhaps as experience with the testing materials accumulated. Other less efficient behaviors however were innovated within the first two hours of testing (Kitahara-Frisch & Norikoshi, 1982). The long latency until innovation reported by Natale et al. (1988) could have been a consequence of the young age of the test subject and the lack of familiarity with tools or enrichment before the start of the experiments. In the case of Manrique and Call (2011), although the number of trials until innovation was relatively high (15), the time until innovation was only 43 min. This example highlights the importance of not only reporting the trial number in which a behavior emerged but also the timing/latency of the innovation. It is unclear why the subjects tested by Tomasello et al. (1987) took so long to innovate raking given that other studies that tested these same behaviors reported short latencies to innovation (Birch, 1945).

Given the known behavioral variation between captive and wild individuals, it is important to consider that the early innovation tendency that we observed in our literature review might not be generalizable to wild populations (unless perhaps in exceptional cases

where wild populations have similarly low predatory pressures and high food availability as captive environments). Furthermore, most of the latency data compiled in our literature search comes from studies investigating orangutan and chimpanzee tool innovation. Such bias in species representation is understandable considering that these two species possess the broadest tool use repertoires among great apes (van Schaik et al., 2003; Whiten et al., 1999). However, multiple studies in captivity have demonstrated that captive gorillas and bonobos can develop tool-using skills of similar proficiency to those observed in chimpanzees and orangutans if provided with suitable enrichment (Gruber & Clay, 2016; Lonsdorf et al., 2009). These studies show that differences in cognitive abilities do not directly explain the lack of tool use in wild gorillas and bonobos, highlighting the need to include these species in more tool experiments in captivity to better understand tool performance and development among great apes.

Species comparisons revealed a larger variation in tool innovation latency among chimpanzees than among orangutans, who were more consistent in their tool innovation times and faster on average than chimpanzees. Manrique and Call (2011) for example, tested chimpanzees and orangutans in their ability to innovate the use of a straw to gain access to a liquid reward. The authors found that it only took three minutes for the first orangutan to innovate straw use whereas it took 43 min for the first chimpanzee to do so. Similarly, orangutan species have been previously found to be more likely to try novel food items than chimpanzees (Forss et al., 2019). These differences in novelty responses have been tentatively explained by the social information hypothesis (Forss et al., 2017), where individuals from more social species (such as chimpanzees) present higher intrinsic neophobia levels than individuals from more solitary species (such as orangutans). To confidently conclude that there exists a general species difference between orangutans and chimpanzees in their latency for tool innovation, future studies could implement a test battery of novel tool behaviors in both species across populations and settings.

By comparing tool innovation latencies among studies that employed different test setups, we found that ape groups took on average longer than individually tested apes to innovate tool behaviors, although the number of trials until innovation was smaller in group settings. This apparent contradiction could be explained if groups were tested in fewer but longer trials than individually tested subjects. Unfortunately we could not corroborate this hypothesis as trial length was often not reported (especially in group tests). In addition, it is important to take into consideration that only one study in our data set applied the same tasks both in group and individual settings (Hopper et al., 2007), meaning that the specific task employed in each experiment could (at least in part) account for the observed differences in innovation times between individually tested and group tested apes. Group testing has been previously praised as a method to improve the ecological validity of cognitive experiments as well as welfare (Cronin et al., 2017). However, testing captive groups also presents certain challenges that might influence experimental results. For example, testing individuals in group settings might limit

the access of low ranking individuals to testing apparatuses or experimental arenas, biasing the sample toward certain individuals in the group. Distractions and interferences directed toward participating individuals can also influence the time that these individuals spend interacting with testing materials. In addition, the need to monitor social interactions among group members and to participate in social behaviors, such as grooming or patrolling in chimpanzees, might reduce the time that individuals dedicate to explore novel tasks. Finally, it should be noted that latencies of individuals tested in group settings might overestimate innovation times. For example, it might occur that an individual tested in a group quickly innovates the behavior within minutes of his/her first contact with the materials but that this first interaction takes place several hours into the trial. Therefore, innovation latencies of group tested individuals might be more informative if reported at the individual level.

In accordance with previous reviews in primate cognition (ManyPrimates et al., 2019), we found that the sample sizes employed in the reviewed studies were generally limited to one or a few testing units, a result that might be partially influenced by our data collection method. Although several of the studies we reviewed tested multiple individuals in a group setting, each group was considered as a single testing unit in our data set. This was because once the first individual in the group innovated the tool behavior then the other individuals could not be considered naïve to the tool behavior anymore (they could have observed the behavioral form). Thus, if multiple innovators would occur in a group, it would not be possible to unequivocally determine by means of which learning mechanisms all innovators except the first one had acquired the tool behavior (Bandini, Motes-Rodrigo, et al., 2020).

Although it would be desirable to test a high number of independent testing units in tool innovation experiments, limited resources often prevent researchers from including large sample sizes in their studies. Innovation studies with small sample sizes (henceforth small *N* studies), however, also provide important and valid results. Small *N* studies can serve as proof of concept of whether individuals from a certain species can learn an unfamiliar tool behavior in the absence of social demonstrations and/or training. Although such studies do not directly show how a tool behavior is actually learned by members of the species, they can inform us about mechanisms that could underlie the learning process. Innovation experiments conducted with small groups also have the advantage that they allow to investigate the diffusion and adoption of the novel behavior by other group members (though not its precise mechanisms), an aspect of innovation that is more difficult to assess the larger the sample size is.

Our review also revealed that the number of publications on the topic of ape tool innovation has been increasing over time and is relatively high since the start of the 2000s. The increase in the last decades of publications focused on the individual learning abilities of captive great apes could indicate a reappraisal in the field of primate cognition of the behavioral baselines employed in the early primate ethology studies (e.g., Koehler, 1925). This reappraisal might have also been influenced by primate studies in the late 80s and



90s that showed that naïve primates could learn relatively complex tool behaviors without the need of observing a model (e.g., Visalberghi, 1987; Westergaard & Suomi, 1994). Furthermore, the increasing number of observations of ape tool behaviors conducted in wild populations in the last decades (Boesch et al., 2009, 2017; Estienne et al., 2017; Hernandez-Aguilar et al., 2007; Pruetz & Bertolani, 2007; Sanz & Morgan, 2007; van Schaik & Fox, 1996) has likely sparked an interest in researchers working both in wild and captive settings to better understand how these behaviors are learnt and incorporated into ape populations.

The experiments reported in our literature review were all conducted with captive ape populations housed mostly in zoos as well as sanctuaries and research facilities. Zoos were specially chosen as testing locations in the last and current decade, with eight of the studies included in our data set being published in the last 2 years alone. These results suggest a scientific perception of zoological institutions as suitable environments to conduct tool innovation experiments. Moreover, the observed reliance on zoos as research host institutions in the last decades likely reflects the global effort made by these centers to become more involved in science communication (Hopper, 2017). There are many reasons why zoos constitute valuable hosting institutions to perform tool innovation studies (and cognitive research in general, Cronin et al., 2017; Hopper, 2017). Foremost, innovation studies are rare in wild populations because novel foraging opportunities or stimuli occur fortuitously (Bandini & Harrison, 2020; Russon et al., 2009). Therefore, it might be that the environment rarely changes enough for the animals to need to innovate new tool behaviors. Alternatively, if innovations do take place they might remain unobserved by researchers or may be only observed when several individuals have adopted the innovation (for an exception see Hobaiter et al., 2014). Experiments conducted in captive environments such as zoos allow researchers to implement controlled and standardized protocols unaltered by environmental factors such as weather conditions or ranging patterns of the study animals. Studies in captivity also allow researchers to investigate scientific questions that are much harder to address in the wild. In captivity, it is possible to provide individual apes or reduced groups with puzzle boxes, apparatuses or materials designed to test for specific cognitive abilities. Similarly, tool innovation experiments are extremely rare in the wild because in most field sites it is not allowed to provide novel objects to the animals as these could alter their natural behavioral repertoire, may cause health concerns and are generally less likely to succeed (but see Forss et al., 2015; Gruber et al., 2016; van de Waal et al., 2010, 2013). Thus, experimental studies conducted in zoological institutions complement research conducted in wild settings and allows tackling scientific questions that would otherwise remain unaddressed.

Although we believe that our review provides important data to inform future tool innovation experiments in great apes, we acknowledge that there are certain limitations to our approach. First of all, we could not assess the effect of task on latency until innovation. Factors such as task complexity or how similar (in terms of form, tool type, or tool material) the innovated tool behavior is relative to the

tool repertoire of the individuals or groups might influence how fast a tool behavior is innovated (see also Schuppli & van Schaik, 2019). Given that it is difficult to assess task complexity and that the behavioral repertoires of the tested apes were not provided in the publications, we could not evaluate the effect of task complexity and familiarity on the timing of innovation (this is also why we refrained from performing statistical analyses on this issue). However, we could descriptively evaluate the type of tasks employed in the studies included in our data set. Given that tool making is rare in most wild primates (Hunt et al., 2013) it seems reasonable that most of the studies included in our data set focused on tool use rather than on tool making. From those studies that investigated both tool using and making, the most commonly tested tool-making behavior was the production of plant tools to fish for liquid or semiliquid out-of-reach rewards (e.g., Boose et al., 2013; Lonsdorf et al., 2009). In all experiments that tested this type of behavior, naïve individuals innovated the solution. On the other hand, all experiments that tested the stone tool making abilities of (unenculturated and untrained) apes, failed to find tool-making innovations of the target behavior (Bandini et al., 2021; Motes-Rodrigo, 2020). Among tool using studies, most experiments focused on innovation of simple technological behaviors (after Shumaker et al., 2011) that involved the use of a single tool, generally a stick or a branch (e.g., Marshall-Pescini & Whiten, 2008; Mulcahy et al., 2005; Visalberghi et al., 1995). Given the negative results of studies testing more complex types of technology (secondary: Bandini et al., 2021; composite: Neadle et al., 2020; Sumita et al., 1985), it is possible that exposure during sensitive learning periods is important or perhaps even necessary for the acquisition of these types of behaviors. Alternatively, individual trial and error learning might not sufficient for naïve individuals to acquire associative tool behaviors at any point (unless perhaps human training takes place).

Another variable that we were not able to account for in our review was the different levels of experience in cognitive experiments that different captive ape populations had. Previous participation in cognitive experiments (particularly those involving tools) might influence how readily apes explore novel apparatuses or experimental setups, affecting in turn how fast individuals innovated the novel tool behaviors (Ebel et al., 2021). The studies included in our data set were conducted in a wide variety of institutions. The apes housed in these institutions differ in their experience participating in cognitive experiments and some institutions have hosted more research projects than others (Hopper, 2017). Only within our data set, we found that zoological institutions such as Bastrop zoo and Leipzig zoo have hosted multiple tool innovation studies (Bandini, Grossmann, et al., 2020; Hanus et al., 2011; Hopper et al., 2015; Whiten et al., 2007). Other institutions such as Twycross Zoo (UK) and Lincoln Park Zoo (USA) present in our data set have also hosted numerous research projects on primate cognition over the years (Hopper, 2017; Neadle et al., 2020).

Finally, it is likely that the results of our review are affected by the publication bias against negative results that plagues academia (Cassey et al., 2004; Jennions & Møller, 2002). Given that it would be

difficult for researchers to publish innovation studies in which the behavior was not innovated (personal observation; but see Bandini & Tennie, 2018; Neadle et al., 2020), we believe that in our review we likely underestimated the number of studies in which no testing unit innovated the target tool behavior. In such cases, longer or even long-term baselines might be particularly valuable.

In conclusion, we found that when great apes acquire novel tool behaviors in the absence of demonstrations or training, this acquisition is very fast, often taking place during the first trial and within the first testing hour. Based on our literature review, we would recommend that future studies investigating innovations of simple tool use behaviors by captive apes implement between 1 and 3 trials with a total cumulative testing time of approximately 2.5 h. As we have shown, past studies suggest that these number of trials and testing duration suffices for the majority of simple tool behaviors to be innovated by naïve apes. For more complex behaviors, such as secondary tool use or the use of composite tools, researchers might need to implement task-specific methodological adjustments. For example, studies investigating composite nut-cracking using hammers and anvils might need to test individuals within potential sensitive learning windows, as claimed for wild chimpanzees (Biro et al., 2003, 2006). Studies investigating the innovation of tool sets that involve more than two elements might also need to implement longer baselines, as the need to use several tools in a specific order might increase the latency until innovation. Future studies might wish to additionally investigate behavioral traits related to or preceding innovations, such as individual exploration tendencies as well as the frequency, nature and latency of object manipulation. Innovation studies might also wish to consider the possibility of a “gray zone of cumulative culture,” where socially mediated individual reinnovation in the past might positively impact future innovations (Tennie et al., 2020). Incorporating these variables into innovation studies would help interpret the observed variation in innovation rates and latencies until innovation among great ape individuals and populations. We hope that our results help researchers to implement more efficient and data-informed tool innovation studies on captive great apes and that this review can serve as a basis to justify testing methods for future studies during the review process.

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## CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

## AUTHOR CONTRIBUTIONS

**Alba Motes-Rodrigo:** conceptualization (equal); data curation (lead); formal analysis (lead); investigation (equal); methodology (equal);

visualization (lead); writing original draft (lead); writing review & editing (equal). **Claudio Tennie:** conceptualization (equal); funding acquisition (lead); investigation (equal); methodology (equal); writing original draft (supporting); writing review & editing (equal).

## DATA AVAILABILITY STATEMENT

All data and code used in this manuscript can be found in the OSF project [https://osf.io/p7r68/?view\\_only=9137d23f65374ea3b23fc5f0da4cb8d8](https://osf.io/p7r68/?view_only=9137d23f65374ea3b23fc5f0da4cb8d8) (Motes-Rodrigo & Tennie, 2021).

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