ROYAL SOCIETY
OPEN SCIENCE

royalsocietypublishing.org/journal/rsos

Cite this article: Bandini E, Harrison R, Hrubesch C, Forss S. 2026 A comparison of tool-use flexibility between captive chimpanzees and bonobos. *R. Soc. Open Sci.* **13**: 251950.
https://doi.org/10.1098/rsos.251950

Received: 18 December 2024
Accepted: 12 January 2026

Subject Category:
Organismal and evolutionary biology

Subject Areas:
behaviour, cognition, evolution

Keywords:
tool use, innovation, tool flexibility, chimpanzees, bonobos

Authors for correspondence:
Elisa Bandini
e-mail: elisa-bandini@hotmail.it
Rachel Harrison
e-mail: rachel.harrison@durham.ac.uk

[†]Elisa Bandini and Rachel Harrison are joint first authors.

Supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8258038.

THE ROYAL SOCIETY
PUBLISHING

A comparison of tool-use flexibility between captive chimpanzees and bonobos

Elisa Bandini[1,2,†], Rachel Harrison[3,†], Christine Hrubesch[4] and Sofia Forss[2]

[1]Interdisciplinary Center for Archaeology and Evolution of Human Behaviour, University of Algarve, Faro, Portugal
[2]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland
[3]University of Durham, Durham, UK
[4]Leintal Zoo, Schwaigern, Germany

EB, 0000-0002-8293-9171; RH, 0000-0001-7876-8886;
SF, 0000-0002-6551-1907

Despite chimpanzees and bonobos sharing close phylogenetic ties to humans, chimpanzees are the more common model species in multiple fields of comparative research. One reason for this bias is the variation in tool repertoire size observed between the two species. Previous studies have examined the factors driving this difference, but few have targeted flexibility in how tools are used. We studied bonobos and chimpanzees under similar conditions in captivity, thus excluding any ecological variation present in these species' natural habitats. We examined whether the species differed in their ability to switch between tools, a trait that may facilitate tool innovation in primates. To do so, we provided the apes with a task that required switching tool type from a rigid stick to a bendable rope to forage successfully. Our data suggest that there are no significant differences in tool-use performance between chimpanzees and bonobos in captivity. However, we found significant differences in the species' exploration tendencies. While chimpanzees fixed their attention on stick tools, bonobos switched their attention more easily towards the rope, potentially due to less functional fixedness. We also found significant within-species differences between institutions. These findings suggest that future research should disentangle intrinsic flexibility in exploration and account for institution and group level effects.

1. Introduction

Though once thought to be unique to humans, the ability to make and use tools has been documented in a diverse range of species and in a variety of contexts [1,2]. Chimpanzees (*Pan troglodytes*) possess the most varied tool-use repertoire of any species outside humans [3], and despite their close phylogenetic relationship, wild bonobos (*Pan paniscus*) use tools only occasionally, and in different contexts from chimpanzees [3,4]. Both species are closely related to humans phylogenetically, with extant chimpanzees and bonobos each sharing some genetic similarities to modern humans that they do not even share with each other, likely due to incomplete lineage sorting [5,6]. Therefore, both species can provide key insights into the evolution of various human traits (within limits [7]), but despite this, historically, chimpanzees have been adopted as the primary models for comparative studies across a range of topics, including tool use [7,8]. By exploring the traits that contribute to the difference in tool use between the two *Pan* species, which shared a common ancestor only 1.5–2.5 million years ago (mya) [9] and diverged from humans between 5 and 7 mya [5], we can better understand when and how humans developed the unique and extensive tool use repertoires we see today.

Reports from the longest running wild bonobo field site (Wamba, in the Democratic Republic of Congo) include observations of only 13 different types of tool use (potentially 14 behaviours in total; see reports of a possible new behaviour at Kokolopori, Democratic Republic of Congo [10]), compared to an estimated 42 thus far reported for chimpanzees [3]. Furthermore, there are differences in the types of tool use observed across the species: bonobo tool use primarily focuses on behaviours within the social and/or play domain [4] (with only one observed extractive foraging behaviour), while chimpanzee tool use primarily focuses on extractive foraging behaviours [11,12]. This discrepancy in size and type of tool repertoires between the species is despite their close genetic relationship [5] and the fact that extant wild bonobos and chimpanzees have comparable dietary needs [13]. To properly uncover whether differences in ecological pressures have caused the observed tool use differences, one would need to cover the evolutionary history of these species' habitats, or alternatively analyse long-term data on how ecological fluctuations shape tool use patterns. Research on extant populations suggests that bonobos may experience less seasonal variability in food abundance compared to chimpanzees [3]; however, the ecological variation in food fluctuations both across and within the two *Pan* species is large and overlapping, which suggests that similar ecological demands apply to the two species, despite occasional reported local foraging patterns [14].

In contrast to what has been observed in the wild, in captivity, most apes, including bonobos, can use tools across contexts and domains [4,15]. This phenomenon has been referred to as the 'captivity bias' or 'captivity effect' and has been suggested to result from developmental effects and the conditions faced by captive apes. This effect is not unique to primates and has also been documented across a variety of other taxa including elephants [16], corvids [17] and bird species [18,19]. The captivity effect may be driven by a variety of factors, including increased close contact with tool-using conspecifics, exposure to humans and their artefacts, and free time due to provisioning and lack of predation [15]. A more extreme version of the captivity effect is 'enculturation', which refers to apes that have been raised by humans from a young age and/or undergone specific human-oriented training over extended periods (e.g. [20,21]). These individuals often demonstrate skills and behaviours that seem to go beyond the natural abilities of unenculturated conspecifics. While some studies with unenculturated captive bonobos and chimpanzees have found that the species perform differently on cognitive test batteries, with bonobos reported to be better at theory of mind and social causality tasks, while chimpanzees outperformed bonobos in tasks that required tools and understanding of physical causality [22], observational reports suggest that tool-use frequency is very similar across these two species in captivity [4].

Previous findings that captive bonobos can use tools in similar ways and frequencies as chimpanzees suggest that bonobos do not lack the general cognitive capacity for tool use in extractive foraging tasks. Therefore, observed differences in the wild could be due to either intrinsic motivation or socio-ecological factors (or a combination of the two), which are altered or absent in captivity. Indeed, in a study on wild bonobo and chimpanzee juveniles, Koops *et al.* [23] showed that predispositions and motivation to manipulate objects were higher in wild chimpanzee infants, as they paid more attention to objects and object-play, relative to wild bonobo infants, suggesting potential developmental roots to the differences in tool-use repertoires later in life.

Therefore, while some differences between the species have been identified, other traits linked to tool use are yet to be tested. In the current study, we aimed to expand on this topic by focusing on

Table 1. Demographic information for the sample from each facility.

species	facility	sex	mean age and range (years)
bonobo	Berlin Zoo	2 females, 1 male	21 (8–36)
	Frankfurt Zoo	5 females, 4 males	25.28 (7.5–66)
	Leipzig Zoo	5 females, 3 males	15.25 (4–26.5)
chimpanzee	Leintal Zoo	10 females, 4 males	20.79 (10–46)
	Ngamba Island	24 females, 16 males	19.94 (8–33)

tool flexibility, as this has been suggested to be a limiting factor for primate innovation (within the extractive foraging context) and has yet to be compared between the two species [24,25]. Here, we refer to tool flexibility as the ability to switch between different types of tools and/or change the usage of tool types according to existing challenges. To flexibly switch between and understand different tool types also requires motivation to engage with various objects in order to identify the distinct physical properties of each tool type (thus potentially requiring higher propensities for object manipulation and general flexibility rather than conservatism or functional fixedness; see [23]). Previous studies in chimpanzees have found surprisingly low levels of behavioural flexibility and higher levels of conservatism [24,26,27], though results vary by task type [28] and between groups of chimpanzees [29]. Currently, there are, to our knowledge, no data on behavioural flexibility in captive bonobos using tool-based paradigms. To identify any potential intrinsic differences between bonobos and chimpanzees in the way they attend to and flexibly switch between tools, we tested bonobos and chimpanzees housed at multiple facilities with similar captive conditions (in which tools and artefacts were present throughout an ape's lifetime). Flexibly switching between tools may be a beneficial behaviour in situations in which new challenges require an individual to perform novel actions using a tool (here referred to as tool innovation). Thus, this study had two main aims.

First, we tested the tool-use performance and tool innovation capabilities (A1) of captive bonobos and chimpanzees when faced with the same (to them) new tool task. The experiment consisted of an easy stick tool-use task and a more demanding rope tool-use challenge, thus allowing us to assess whether each species was able to flexibly switch between the two tool types and tasks. The second aim (A2) of the study was to examine whether there were differences in underlying motivational processes, like object-directed exploration, and how such traits may link to potential differences in tool usage.

2. Methods

2.1. Subjects

Data collection on bonobos was conducted between April and August 2017 at the following three German zoos: Berlin Zoo ($n = 3$), Frankfurt Zoo ($n = 9$) and the Wolfgang Köhler Primate Research Centre ($n = 8$) located within Leipzig Zoo. The facilities were selected as they allowed us to test the apes individually. Individual demographic details (sex, age at testing and rearing background) can be found in electronic supplementary material, table S1. Data collection on chimpanzees was conducted between September and October 2017 at Ngamba Island Chimpanzee Sanctuary ($n = 40$) located in Lake Victoria, Uganda, and at Leintal Zoo ($n = 14$), Germany. In Leintal Zoo, three chimpanzees did not interact with the task at all and thus were excluded from our analyses. See table 1 for an overview of the demographic information. In both the bonobo and the chimpanzee sample, we had individuals that were mother-reared within their peer groups of conspecifics at the zoo, but also individuals that had lost their mothers early during ontogeny and therefore were human-reared and afterwards integrated into a group of conspecifics.

2.2. Procedure

We tested the apes individually in their familiar main enclosures or sleeping quarters. All efforts were made so that the apes could enter the test location voluntarily to avoid any confounding effects from stress due to isolation from the group. Subjects were fed their regular amount of food on testing days and were never water deprived. Testing took place roughly 1–2 hours after their morning feeding.

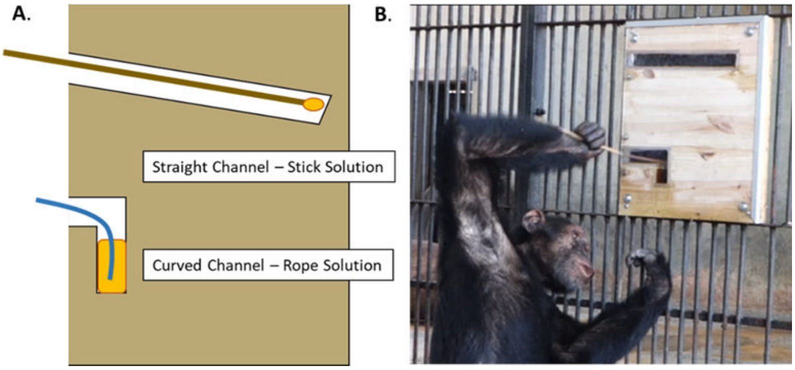

Figure 1. (A) Illustration of the two different tool challenges presented to the chimpanzees and bonobos: straight channel (tool behaviour: re-use of stick to extract honey) and curved channel (tool behaviour: use the rope tool (provided on the floor) to fish honey). (B) Chimpanzee at Ngamba Island Sanctuary inserting the stick tool into the curved channel (photo credit: S.F.).

The tool-use task consisted of a wooden and Plexiglas honey trap, featuring two different channels visible to the ape: a straight channel and a curved one (figure 1) as well as two distinct tools. This chimpanzee dataset has previously been used to assess facility differences on physical cognition in captive chimpanzees [30], and this task was also part of a cognitive test battery with captive orangutans addressing tool use skills across species and rearing conditions [31,32]. We provided the apes with three pieces of each tool type (stick and rope). The straight channel was empty, but at the start of the experiment, a stick tool with the tip dipped in honey was inserted, and as such, a small amount of honey could still be retrieved from the end of the straight channel when re-inserting the stick after tasting the first honey. This was done to allow the apes to gain an understanding of the properties of the stick tool, prior to potentially flexibly switching tool strategy for the curved channel. At the same time, retrieving only small amounts of honey with the stick tool was intended to increase the apes' motivation to explore the curved channel, which was more difficult to solve, and thus would require innovating a novel tool action [32]. Task performance was measured by (i) whether or not the ape inserted the stick again (or any of the additional two provided sticks) into the straight channel (referred to as 're-insertion stick channel' in our dataset) and/or (ii) whether or not the ape innovated the rope solution by inserting the rope tool into the curved channel, being rewarded with honey sticking to the rope (referred to as 'solved rope solution' in the dataset). There was no pre-training for this task, and each ape was presented the task only once. Each test lasted 10 min. All tests were video recorded using one to two SONY HDR-CX200 Handy cameras, depending on the need due to angles and visibility.

2.3. Data coding and statistical analyses

We extracted all detailed behaviours (see ethogram in electronic supplementary material, table S2) expressed by the apes during testing from the video recordings using Mangold Interact, v. 9, and 15% of the test videos were inter-rater reliability coded and showed a good Cohen's Kappa value of 0.81 [33]. From the videos, we coded task performance: whether or not the ape re-inserted the stick in the straight channel and assessed tool flexibility by coding whether the ape innovated the rope solution (inserting the rope to two-thirds into the curved channel). In addition, we also coded all detailed exploration actions: number of times an ape inserted a stick into either channel, number of times the ape inserted a finger into any of the two channels and each time the ape touched and/or manipulated any of the provided tool items lying on the floor next to the apparatus (electronic supplementary material, table S2).

3. Results

3.1. Species and facility differences in tool-use performance

We fitted generalized linear mixed models (GLMMs) with binomial error structures and logit link functions. The outcome variable in both models was success in re-inserting the stick (coded as 'success' in the straight channel task) and innovating the rope solution ('success' in the curved channel task), with failure coded as 0 and success coded as 1. Model 1 included Task Type (straight channel versus curved channel), Age (z-transformed to a mean of 0 and standard deviation of 1), Sex (female versus male) and Species (bonobo versus chimpanzee) as predictors, with random effects of both Individual ($n = 74$) and Facility ($n = 5$) to account for repeated measures (as each individual contributed two data points to the dataset—success or failure on each of the straight channel and curved channel tasks). Model 2 was identical but included Facility rather than Species as a predictor variable and did not include a random effect of Facility. As only one species was tested in each facility, both predictors could not be included as main effects in the same model. The two models were compared using a likelihood ratio test (test 'Chisq' in the R function 'anova'), which revealed that Model 2 (containing Facility as a predictor) was a significantly better fit to the data than Model 1 (containing Species as a predictor) ($X^2 = 10.58$, $p = 0.005$). No significant effect of Species was found in Model 1 ($\beta = -0.31$, $p = 0.74$). An additional model, including the effect of rearing history, is presented in the electronic supplemental material but found no effect of rearing history upon performance. Further examination of results was therefore restricted to Model 2.

Model 2 was a significantly better fit to the data than a null model containing only the random effect of Individual ($X^2 = 57.11$, $p < 0.001$). The model was assessed for multicollinearity using the function 'vif' in the R package 'car', with a maximum observed value of 1.22, indicating no issues.

There was a significant effect of Task Type ($\beta = 2.77$, $p < 0.001$), indicating that individuals were more likely to solve the straight channel task by re-inserting the stick than to solve the curved channel task, which required innovating the rope solution. There was no significant effect of either Age or Sex. The facility impacted individuals' likelihood of solving both task types (overall significance calculated using the 'Anova' function in the package 'car': $X^2 = 11.68$, $p = 0.020$). A *post hoc* Tukey test revealed that individuals at Ngamba Island were significantly more likely to successfully solve both tasks than individuals at Leintal Zoo ($\beta = 2.21$, $p = 0.013$). No other significant between-facility differences were found (see figure 2).

3.2. Order of task success

Of 24 individuals who solved both the straight and curved channel tasks, 21 reinserted the stick tool into the straight channel (solving that task) before inserting the rope tool into the curved channel (solving that task). Of the three individuals who solved the curved channel task first, two were bonobos and one was a chimpanzee. One additional individual (a bonobo) solved only the curved channel task and never reinserted the stick into the straight channel. A Fisher's exact test revealed no difference between the species in the number of individuals who solved the curved channel task before the straight channel task ($p = 0.53$), and in the majority of individuals, reinsertion of the stick (solving the straight channel task) occurred before insertion of the rope (solving the curved channel task).

3.3. Tool type exploration

We fitted GLMMs with Poisson error structures and log link functions. The outcome variable in both models was the count of exploration events, with Tool Type (stick versus rope), Sex, Age (z-transformed to a mean of 0 and standard deviation of 1) and Species (chimpanzee versus bonobo) as predictor variables. An interaction between Tool Type and Species was included to test whether bonobos or chimpanzees explored the different tool types at different frequencies. A random effect of Individual ($n = 74$) was included to account for repeated measures (as each individual contributed two data points to the dataset—their counts of stick and rope tool explorations).

This model was a significantly better fit to the data than a null model containing only the random effect of individual ($X^2 = 994.13$, $p < 0.001$). The model was assessed for multicollinearity using the function 'vif' in the R package 'car', with a maximum value of 3.84 (observed in the terms involved in the interaction), indicating no issues. The model was assessed for overdispersion using the function 'testDispersion' in the R package DHARMa, and no significant overdispersion was found (dispersion = 0.66, $p = 0.54$). Exploration frequencies varied by both Species and Tool Type. Bonobos explored using the stick more frequently than they did the rope ($\beta = 0.88$, $p < 0.001$), but this effect was significantly stronger in chimpanzees (significant interaction between Species and Tool Type, $\beta = 1.55$, $p < 0.001$), indicating that chimpanzees explored using the stick tool at even higher frequencies than bonobos did. Chimpanzees and bonobos explored using the rope tool at similar rates ($\beta = -0.47$, $p = 0.072$; see figure 3).

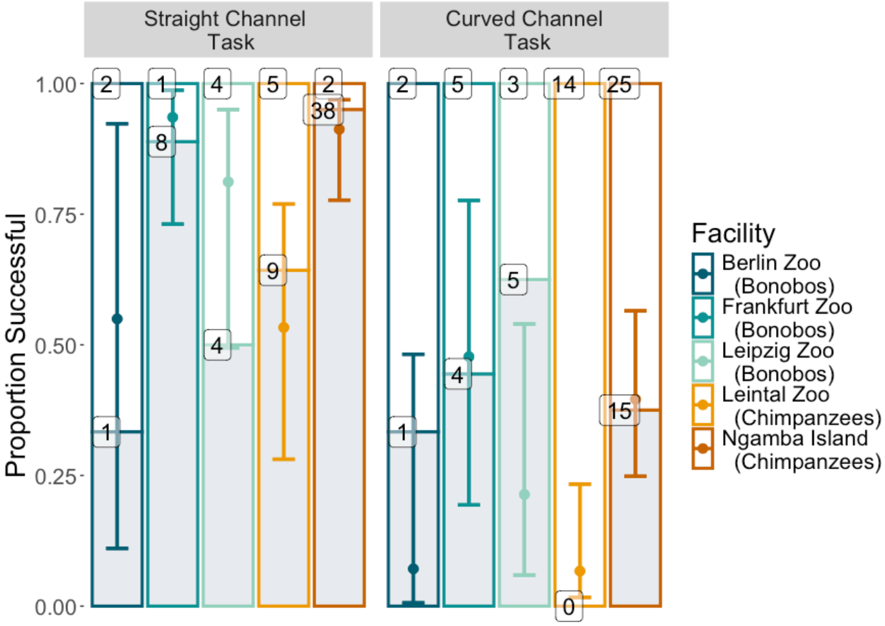

Figure 2. Proportion of individuals who solved the straight and curved channel tasks. Grey bars represent the observed proportions, points represent the model-predicted values and error bars show the upper and lower confidence intervals of the model-predicted values. The count of successful individuals can be found at the upper end of each bar, and the number of unsuccessful individuals can be found at the top.

3.4. Stick use

We fitted a GLMM with Poisson error structure and log link function to analyse whether there were any species differences in the frequency with which individuals used the stick to probe the straight versus curved channels. The outcome variable was the count of probing events using the stick, with Task Type (straight versus curved), Sex, Age (*z*-transformed to a mean of 0 and standard deviation of 1) and Species (chimpanzee versus bonobo) as predictor variables. An interaction between Task Type and Species was included to test whether bonobos or chimpanzees explored the different task types at different frequencies. A random effect of Individual ($n = 74$) was included to account for repeated measures (as each individual contributed two data points to the dataset—their counts of straight and curved problem explorations).

This model was a significantly better fit to the data than a null model containing only the random effect of Individual ($X^2 = 44.56$, $p < 0.001$). The model was assessed for multicollinearity using the function ‘vif’ in the R package ‘car’, with a maximum value of 1.33, indicating no issues. The model was assessed for overdispersion using the function ‘testDispersion’ in the R package DHARMa, and no significant overdispersion was found (dispersion = 0.51, $p = 0.44$).

Exploration frequencies varied by both Species and Task Type. Both species showed higher exploration rates using the stick tool for the curved channel than the straight, but this effect was significantly stronger in the bonobos (Task Type effect in chimpanzees $\beta = 0.18$, $p = 0.003$; Task Type and Species interaction in bonobos $\beta = 0.58$, $p = 0.003$; see figure 4).

3.5. Time spent at the apparatus

We fitted a linear mixed model to assess whether there was a species difference in the overall time individuals spent at the task. The outcome variable was the amount of time spent (in minutes) active at the task, with Species (chimpanzee versus bonobo), Age (*z*-transformed to a mean of 0 and standard deviation of 1) and Sex as predictor variables, and a random effect of Facility. The model indicated that none of these predictor variables influenced time spent at the task, and the full model was not a better fit to the data than a null model containing only the random effect of Facility ($X^2 = 5.12$, $p = 0.16$).

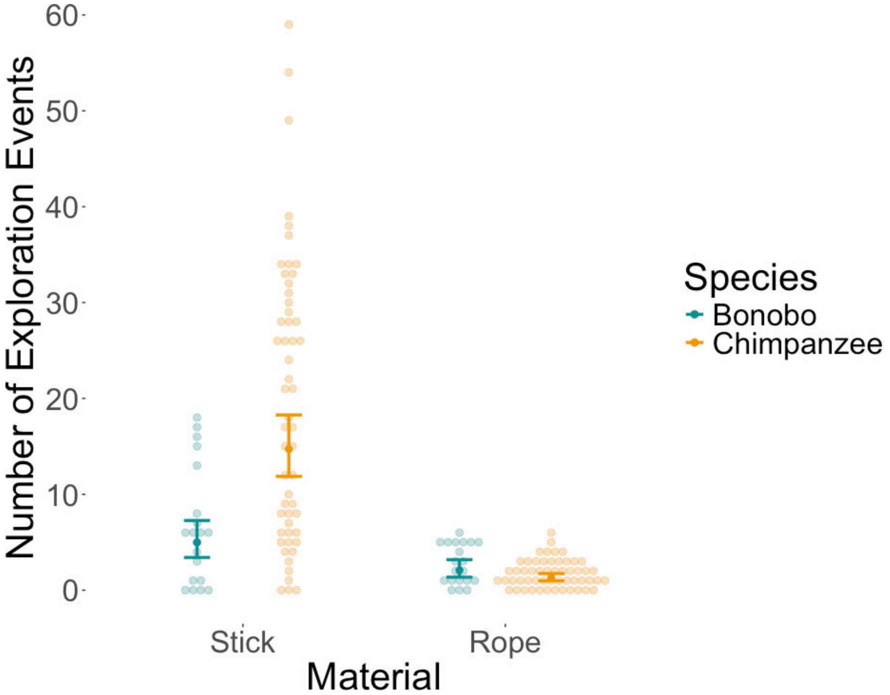

Figure 3. The number of exploration events by the subjects. Points represent the number of exploration events using each tool type by individual subjects, coloured by species (bonobos versus chimpanzees). Solid points show the model-predicted values, with error bars showing the upper and lower confidence intervals.

4. Discussion

4.1. A1: Comparing tool-use performance between captive chimpanzees and bonobos when faced with the same novel tool challenge

Here, we provided an experimental assessment of tool-use performance across captive chimpanzees and bonobos from multiple facilities, in which all groups were faced with the same novel tool challenge. Our data showed that both species were equally motivated to manipulate the apparatus, with no difference found in the time they spent interacting with the task, and that both species were more likely to reinsert the stick into the straight channel than to successfully innovate usage of the rope tool to extract honey from the more challenging curved channel. This aligns with previous results from orangutans (*Pongo abelii* and *Pongo pygmaeus*), and thus the perceived task difficulty seems to generalize across great apes [31]. Despite clear differences in frequency and type of tool use repertoires in the wild, in captivity, we did not find any species difference between chimpanzee and bonobo overall tool performance, in line with some previous findings (e.g. [4,34] but see [22]). This was true for both the reinsertion of the stick (indicating understanding of its match with the straight channel) and the apes' ability to flexibly switch to another tool type, and thereby innovate a rope tool solution to extract honey from the curved channel. This was despite the fact that the tool use tasks we provided were within the extractive foraging domain, which in the wild elicits more tool use in chimpanzees relative to bonobos [11,12]. Our data suggest, therefore, that the general cognitive abilities for tool manipulation and problem-solving do not differ between the species in captivity and are not subject to innate species differences.

The captivity effect [15] may have boosted the performance of both species in our study, resulting in no apparent species differences in capabilities. In particular, captivity seems to facilitate tool use in bonobos who do not typically use tools in foraging contexts in the wild [15,35]. Indeed, previous research in two other great ape species (Sumatran and Bornean orangutans, *Pongo abelii* and *Pongo pygmaeus*) found that individual background and orientation towards humans, acquired during their time in captivity, influenced performance on the same tool use task [31,36] and that Bornean orangutans, who do not use stick tools in the wild, were able to solve this task in captivity at a similar level to their tool-using Sumatran sister species [32]. As such, our study does not support the notion of any intrinsic differences in the two species' capacity for tool use, but rather points towards socio-ecological

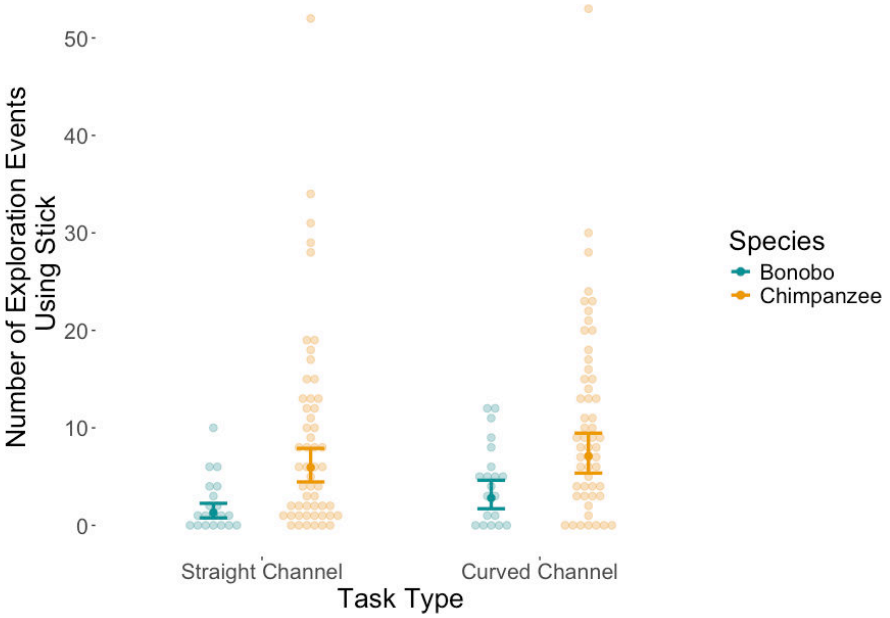

Figure 4. The number of exploration events using the stick tool by individuals. Points represent the number of exploration events of each task type by individual subjects, coloured by species (bonobos versus chimpanzees). Solid points show the model-predicted values, with error bars showing the upper and lower confidence intervals.

factors altered by life in captivity equalling out any potential differences in tool flexibility existing in wild chimpanzees and bonobos.

However, it remains unclear which factors drive the observed enhancement in tool use performance. The potential complexity of the captivity effect is perhaps exemplified by the fact that we identified a difference in performance between chimpanzees living in different facilities (chimpanzees housed in Leintal Zoo versus those housed at Ngamba Island Sanctuary), demonstrating that it is not captivity *per se* that impacts performance, but rather that there may be factors that differ between captive care facilities that influence tool use behaviour. Our finding is consistent with previous published data from the same dataset [30] and with the hypothesis that experience in research influences cognition and performance in captive primates [37]. One previous study also identified this effect (among others) even within facility at Leipzig Zoo, with subjects (across species) who had participated in more experiments performing better in subsequent tasks [38]. Indeed, the chimpanzees housed at Ngamba Island Sanctuary, who participated in more research studies over time than their counterparts at Leintal Zoo [30], performed significantly better. While there was no significant difference in success rates between the three bonobo facilities, success rates across these facilities still varied. Beyond previous experimental experience, differences in performance between facilities may be a reflection of various other factors, such as time spent in captivity (as previously shown in the same sample [30]), differences in rearing history [39] and motivational traits, such as exploration tendency and persistence [40]. Even within a relatively large sample, it is challenging to explore all the potential factors that may influence performance on tool use tasks and indeed cognitive tasks more broadly. Future research should continue to focus on disentangling the experience factors that may impact performance within captive populations and ideally include multiple facilities in experiments (see also [37]).

4.2. A2: Examining underlying cognitive processes: exploration tendency and tool-use flexibility between captive chimpanzees and bonobos

Our study also investigated whether chimpanzees and bonobos differed in their attention to objects, as such variation may underlie the emergence of physical innovations [24,25]. In this study, in order to continue to successfully retrieve honey, the apes had to switch from the easy stick dipping behaviour to the harder challenge of innovating a new tool solution by fitting the rope in the curved channel. Across both behaviours, both species, regardless of facility, explored and manipulated the apparatus using the provided stick tool more than the rope tool. However, this effect was stronger in the chimpanzee sample. Thus, in line with previous studies that identified conservatism in other captive chimpanzee populations [24], the chimpanzees in this study fixated on the stick as a potential tool more than the bonobos did. Yet, to what extent individual conservatism relates to behavioural flexibility remains to be assessed. These data are also consistent with observations from wild chimpanzee populations, in which the use of stick probes is considered a universal behaviour and is absent from only one field site [11,41] and young chimpanzees become increasingly focused on stick manipulation with age [23], as well as the finding of high levels of functional fixedness when it comes to tool types [24,42]. Conversely, wild bonobos have never been observed using stick probes [4,43], perhaps raising the question of differing levels of intrinsic motivation to interact with certain tool types [23].

It has previously been suggested that species that regularly use tools in the wild may have an 'attentional bias towards tools' [44, p. 133], but this hypothesis raises the question of what type of object constitutes a 'tool' for a given species. One eye-tracking study found that captive chimpanzees have a stronger attentional bias towards action target objects (objects included tools, food and toys) relative to bonobos [45], but our findings could be interpreted to suggest that chimpanzees may have a more specific attentional bias towards sticks as potential tools, thus driving their tendency to explore using the stick tool rather than the rope tool to a greater extent than the bonobos. This could contribute to the near-ubiquity of stick tool use observed in wild populations (though we note the complete lack of stick tool use so far observed in one wild population [46]).

In our study, as well as exploring using the two tool types more equally than the chimpanzees, the bonobos were more willing to modify their strategy based on the task challenge. When using the stick tool, despite having overall lower exploration rates than the chimpanzees, bonobos focused their exploration more towards the curved channel than chimpanzees did, an approach that was necessary to maximize the amount of honey they could retrieve. Previous studies using non-tool-based paradigms have found no difference between the two species in terms of general behavioural flexibility [28,47], but our findings suggest that the two species may differ in attentiveness to tool types, with chimpanzees remaining the more conservative/functionally fixed *Pan* species. These data are somewhat surprising, as behavioural inflexibility has been suggested to limit behavioural innovation, which seems inconsistent with the fact that wild chimpanzees have a larger and more varied tool repertoire than bonobos. Although, conversely, a lack of innovation may explain why chimpanzee behavioural repertoires seem to remain stable over time. Persistence has also been shown to be key to problem-solving in a range of species [48,49], and the relative contribution of behavioural flexibility versus persistence in tool innovation has yet to be understood. Continuing to exploit a previously used resource may lead to the refinement of tool use techniques, while exploring the surrounding environment may lead to the discovery of new resource opportunities. Both processes may be important for tool innovation in the wild. A bias towards continuing to try to exploit known resources using existing tool techniques may also help explain why chimpanzee behaviours seem to remain relatively static over long periods of time (e.g. [50]).

5. Conclusion

In summary, we did not find any significant differences between captive chimpanzees and bonobos in their tool use performance when faced with the same problems and when tested under the comparable environmental conditions offered by captivity. However, we did identify variance within the species' abilities to flexibly switch between tools and attention towards the different challenges the apparatus presented. Chimpanzees seemed to focus more on sticks, which could suggest a higher functional fixedness in chimpanzee tool cognition relative to bonobos, but may also reflect an attentional bias towards certain types of potential tool materials, which could lead to higher rates of tool use in the wild. Bonobos, on the other hand, showed a greater tendency to explore using the rope tool, with exploration rates using the two tool types more similar in bonobos than in chimpanzees. While both species used the stick tool to explore the curved channel, presenting the higher reward, more than the straight channel, this difference was greater in bonobos, perhaps suggesting less functional fixedness in bonobos. In addition, our study confirmed previous findings with regard to the facility in which the subjects were living [30], which was an even stronger predictor of success than species type. This finding holds important implications for our understanding of captive ape cognition, as it suggests that the current approach of treating all captive apes as cognitively and behaviourally 'equal' may be misleading (see also [37]). Future studies should include different populations housed across facilities to ensure a comprehensive approach to data collection, and potential differences in behaviour and cognition across institutions should be measured and quantified (see also [37]). Such an approach would also allow researchers to begin to identify the factors that lead to the 'captivity effect' in primate tool use, further exemplified in our study as we found that in captivity, bonobos were as motivated and able to use tools as chimpanzees, even though wild bonobos do not show the same tool repertoires or predispositions as chimpanzees [23]. Identifying the factors that promote tool use even in non-habitual tool-using species in captivity may also provide an indication of the factors that contribute to the emergence of tool use in the wild. Future studies should focus on further testing the external and intrinsic factors underlying tool use abilities and flexibility of both extant members of the *Pan* genus and other great apes.

Ethics. The honey trap task used in this study represented a non-invasive method with severity degree zero, and only behavioural observations were made (i.e. no human interaction/interference was required during testing). All tests complied with the ethical principles set by the zoos where data were collected and were supported by the BIAZA Animal Care Committee (British and Irish Association for Zoos and Aquariums). For the data collected at Ngamba Island Wildlife Sanctuary in Uganda, we received ethical approval by UWA, Ugandan Wildlife Authority (UWA/COD/95/06) and the National Council for Science and Technology (UNCST; reference number NS27ES).

Data accessibility. All data can be accessed at the dedicated Open Science Framework page: https://osf.io/3gzx6/?view_only=43bd6183147348009463ded363493581.

Electronic supplementary material is available online [51].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. E.B.: project administration, validation, visualization, writing—original draft, writing—review and editing; R.H.: formal analysis, writing—review and editing; C.H.: data curation, methodology; S.F.: conceptualization, funding acquisition, methodology, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. Swiss National Science Foundation, grant nos. P2ZHP3_171902 and PZ00P3_202052 (S.F.), Einstein Award (E.B., S.F.), UZH Postdoc grant (E.B.). R.H. is supported by a Leverhulme Early Career Fellowship (ECF-2023-039). E.B. is funded by the European Union (ERC PRIMERS project number 101161975). Views and opinions expressed are however those of the author(s) only and do not necessarily reflect those of the European Union or the European Research Council Executive Agency. Niether the European Union nor the the granting authority can be held responsible for them.

Acknowledgements. We are grateful to all our collaborating facilities and institutions that hosted this study, with special thanks to the caregivers helping us out with the logistics during experimental set-ups.

References

1. Bentley-Condit VK, Smith EO. 2010 Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour* **147**, 185–221. (doi:10.1163/000579509X12512865686555)
2. Shumaker RW *et al*. 2011 *Animal tool behavior: the use and manufacture of tools by animals*. Baltimore, MD: Johns Hopkins University Press. (doi:10.1353/book.98237)
3. Furuichi T, Sanz C, Koops K, Sakamaki T, Ryu H, Tokuyama N, Morgan D. 2015 Why do wild bonobos not use tools like chimpanzees do? *Behaviour* **152**, 425–460. (doi:10.1163/9789004304178_010)
4. Gruber T, Clay Z, Zuberbühler K. 2010 A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the *Pan* lineage. *Anim. Behav*. **80**, 1023–1033. (doi:10.1016/j.anbehav.2010.09.005)
5. Prüfer K *et al*. 2012 The bonobo genome compared with the chimpanzee and human genomes. *Nature* **486**, 527–531. (doi:10.1038/nature11128)
6. Rogers J, Gibbs RA. 2014 Comparative primate genomics: emerging patterns of genome content and dynamics. *Nat. Rev. Genet*. **15**, 347–359. (doi:10.1038/nrg3707)
7. Bandini E, Harrison RA, Motes-Rodrigo A. 2022 Examining the suitability of extant primates as models of hominin stone tool culture. *Humanit. Soc. Sci. Commun*. **9**, 74. (doi:10.1057/s41599-022-01091-x)
8. Carvalho S, Beardmore-Herd M. 2019 Technological origins: primate perspectives and early hominin tool use in Africa. In *Oxford research encyclopedia of African history*. See https://oxfordre.com/africanhistory/view/10.1093/acrefore/9780190277734.001.0001/acrefore-9780190277734-e-75.
9. Langergraber KE *et al*. 2012 Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proc. Natl Acad. Sci. USA* **109**, 15716–15721. (doi:10.1073/pnas.1211740109)
10. Samuni L, Lemieux D, Lamb A, Galdino D, Surbeck M. 2022 Tool use behavior in three wild bonobo communities at Kokolopori. *Am. J. Primatol*. **84**, e23342. (doi:10.1002/ajp.23342)
11. Whiten A *et al*. 2001 Charting cultural variation in chimpanzees. *Behaviour* **138**, 1481–1516. (doi:10.1163/156853901317367717)
12. McGrew WC. 1992 *Chimpanzee material culture: implications for human evolution*. New York, NY: Cambridge University Press.

13. Boesch C. 2002 Behavioural diversity in *Pan*. In *Behavioural diversity in chimpanzees and bonobos* (eds C Boesch, G Hohmann), pp. 1–8, 1st edn. New York, NY: Cambridge University Press. (doi:10.1017/CBO9780511606397.002)
14. Gruber T, Clay Z. 2016 A comparison between bonobos and chimpanzees: a review and update. *Evol. Anthropol. Issues News Rev.* **25**, 239–252. (doi:10.1002/evan.21501)
15. Haslam M. 2013 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. *Phil. Trans. R. Soc. B* **368**, 20120421. (doi:10.1098/rstb.2012.0421)
16. Chevalier-Skolnikoff S, Liska J. 1993 Tool use by wild and captive elephants. *Anim. Behav*. **46**, 209–219. (doi:10.1006/anbe.1993.1183)
17. Bird CD, Emery NJ. 2009 Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proc. Natl Acad. Sci. USA* **106**, 10370–10375. (doi:10.1073/pnas.0901008106)
18. Auersperg AMI, Szabo B, von Bayern AMP, Kacelnik A. 2012 Spontaneous innovation in tool manufacture and use in a Goffin's cockatoo. *Curr. Biol*. **22**, R903–R904. (doi:10.1016/j.cub.2012.09.002)
19. Huber L, Gajdon GK. 2006 Technical intelligence in animals: the kea model. *Anim. Cogn*. **9**, 295–305. (doi:10.1007/s10071-006-0033-8)
20. Buttelmann D, Carpenter M, Call J, Tomasello M. 2007 Enculturated chimpanzees imitate rationally. *Dev. Sci*. **10**, F31–F38. (doi:10.1111/j.1467-7687.2007.00630.x)
21. Tomasello M, Savage-Rumbaugh S, Kruger AC. 1993 Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Dev*. **64**, 1688–1705.
22. Herrmann E, Hare B, Call J, Tomasello M. 2010 Differences in the cognitive skills of bonobos and chimpanzees. *PLoS One* **5**, e12438. (doi:10.1371/journal.pone.0012438)
23. Koops K, Furuichi T, Hashimoto C. 2015 Chimpanzees and bonobos differ in intrinsic motivation for tool use. *Sci. Rep*. **5**, 11356. (doi:10.1038/srep11356)
24. Harrison RA, Whiten A. 2018 Chimpanzees (*Pan troglodytes*) display limited behavioural flexibility when faced with a changing foraging task requiring tool use. *PeerJ* **6**, e4366. (doi:10.7717/peerj.4366)
25. Bandini E, Harrison RA. 2020 Innovation in chimpanzees. *Biol. Rev*. **95**, 1167–1197. (doi:10.1111/brv.12604)
26. Hrubesch C, Preuschoft S, van Schaik C. 2009 Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Anim. Cogn*. **12**, 209–216. (doi:10.1007/s10071-008-0183-y)
27. Davis SJ, Schapiro SJ, Lambeth SP, Wood LA, Whiten A. 2019 Behavioral conservatism is linked to complexity of behavior in chimpanzees (*Pan troglodytes*): implications for cognition and cumulative culture. *J. Comp. Psychol*. **133**, 20–35. (doi:10.1037/com0000123)
28. Manrique HM, Völter CJ, Call J. 2013 Repeated innovation in great apes. *Anim. Behav*. **85**, 195–202. (doi:10.1016/j.anbehav.2012.10.026)
29. Harrison RA, van Leeuwen EJC, Whiten A. 2021 Chimpanzees' behavioral flexibility, social tolerance, and use of tool-composites in a progressively challenging foraging problem. *iScience* **24**, 102033. (doi:10.1016/j.isci.2021.102033)
30. Forss SIF, Motes-Rodrigo A, Hrubesch C, Tennie C. 2020 Chimpanzees' (*Pan troglodytes*) problem-solving skills are influenced by housing facility and captive care duration. *PeerJ* **8**, e10263. (doi:10.7717/peerj.10263)
31. Damerius LA *et al*. 2017 Orientation toward humans predicts cognitive performance in orang-utans. *Sci. Rep*. **7**, 12. (doi:10.1038/srep40052)
32. Forss SIF, Willems E, Call J, van Schaik CP. 2016 Cognitive differences between orang-utan species: a test of the cultural intelligence hypothesis. *Sci. Rep*. **6**, 30516. (doi:10.1038/srep30516)
33. Landis JR, Koch GG. 1977 The measurement of observer agreement for categorical data. *Biometrics* **33**, 159–174.
34. Herrmann E, Wobber V, Call J. 2008 Great apes' (*Pan troglodytes, Pan paniscus, Gorilla gorilla, Pongo pygmaeus*) understanding of tool functional properties after limited experience. *J. Comp. Psychol*. **122**, 220–230. (doi:10.1037/0735-7036.122.2.220)
35. Schaik CPV. 2015 *The primate origins of human nature*. Hoboken, NJ: John Wiley & Sons.
36. Damerius LA, Graber SM, Willems EP, van Schaik CP. 2017 Curiosity boosts orang-utan problem-solving ability. *Anim. Behav*. **134**, 57–70. (doi:10.1016/j.anbehav.2017.10.005)
37. Bandini E, Girish S, Barnes P, Boot M, Tennie C, Forss S. 2025 The biases in captive chimpanzee cognitive research: first insights from the ape research index (ARI) database. *Ethology* **131**, 133–141. (doi:10.1111/eth.70007)
38. Bohn M, Eckert J, Hanus D, Lugauer B, Holtmann J, Haun DBM. 2023 Great ape cognition is structured by stable cognitive abilities and predicted by developmental conditions. *Nat. Ecol. Evol*. **7**, 927–938. (doi:10.1038/s41559-023-02050-8)
39. Brent L, Bloomsmith MA, Fisher SD. 1995 Factors determining tool-using ability in two captive chimpanzee (*Pan troglodytes*) colonies. *Primates* **36**, 265–274. (doi:10.1007/bf02381352)
40. Massen JJM, Antonides A, Arnold AMK, Bionda T, Koski SE. 2013 A behavioral view on chimpanzee personality: exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *Am. J. Primatol*. **75**, 947–958. (doi:10.1002/ajp.22159)
41. Mugisha S, Zuberbühler K, Hobaiter C. 2016 First observation of *Dorylus* ant feeding in Budongo chimpanzees supports absence of stick-tool culture. *Primates* **57**, 389–394. (doi:10.1007/s10329-016-0533-3)
42. Ebel SJ, Völter CJ, Call J. 2021 Prior experience mediates the usage of food items as tools in great apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla*, and *Pongo abelii*). *J. Comp. Psychol.* **135**, 64–73. (doi:10.1037/com0000236)
43. Hohmann G, Fruth B. 2003 Culture in bonobos? Between-species and within-species variation in behavior. *Curr. Anthropol*. **44**, 563–571. (doi:10.1086/377649)
44. Amodio P, Jelbert SA, Clayton NS. 2018 The interplay between psychological predispositions and skill learning in the evolution of tool use. *Curr. Opin. Behav. Sci*. **20**, 130–137. (doi:10.1016/j.cobeha.2018.01.002)

45. Kano F, Hirata S, Call J. 2015 Social attention in the two species of *Pan*: bonobos make more eye contact than chimpanzees. *PLoS One* **10**, e0129684. (doi:10.1371/journal.pone.0129684)

46. Gruber T, Muller MN, Strimling P, Wrangham R, Zuberbühler K. 2009 Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Curr. Biol*. **19**, 1806–1810. (doi:10.1016/j.cub.2009.08.060)

47. Manrique HM, Call J. 2015 Age-dependent cognitive inflexibility in great apes. *Anim. Behav*. **102**, 1–6. (doi:10.1016/j.anbehav.2015.01.002)

48. Jacobson SL, Puitiza A, Snyder RJ, Sheppard A, Plotnik JM. 2022 Persistence is key: investigating innovative problem solving by Asian elephants using a novel multi-access box. *Anim. Cogn*. **25**, 657–669. (doi:10.1007/s10071-021-01576-3)

49. Chow PKY, Lea SEG, Leaver LA. 2016 How practice makes perfect: the role of persistence, flexibility and learning in problem-solving efficiency. *Anim. Behav*. **112**, 273–283. (doi:10.1016/j.anbehav.2015.11.014)

50. Mercader J, Panger M, Boesch C. 2002 Excavation of a chimpanzee stone tool site in the African rainforest. *Science* **296**, 1452–1455. (doi:10.1126/science.1070268)

51. Bandini E, Harrison R, Hrubesch C, Forss S. 2026 Supplementary material from: A comparison of tool-use flexibility between captive chimpanzees and bonobos. Figshare. (doi:10.6084/m9.figshare.c.8258038)