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Wild chimpanzees *(Pan troglodytes schweinfurthii)* use tools to access out of reach water

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Abstract

The use of tools to drink water is well-documented in wild chimpanzees, but the specific function of this behavior is unclear. Here we use a large dataset of drinking behaviors spanning 14 years of observation from the Kanyawara community of chimpanzees living in Kibale National Park, Uganda, in order to test two possible functions of leaf-sponges and other drinking tools. On the one hand, chimpanzees may use tools to access water that is hard to reach, which predicts that chimpanzees will preferentially use tools to drink at tree holes and crevices compared to all other locations. Conversely, chimpanzees may use these tools to filter stagnant water, in which case they would use tools more often at holes and puddles compared to running water sources (e.g., streams). We compared both likelihood of using a tool to drink at different locations, as well as

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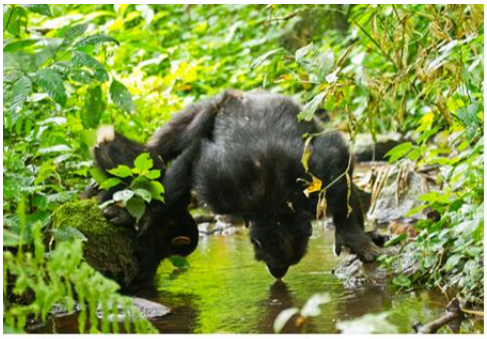
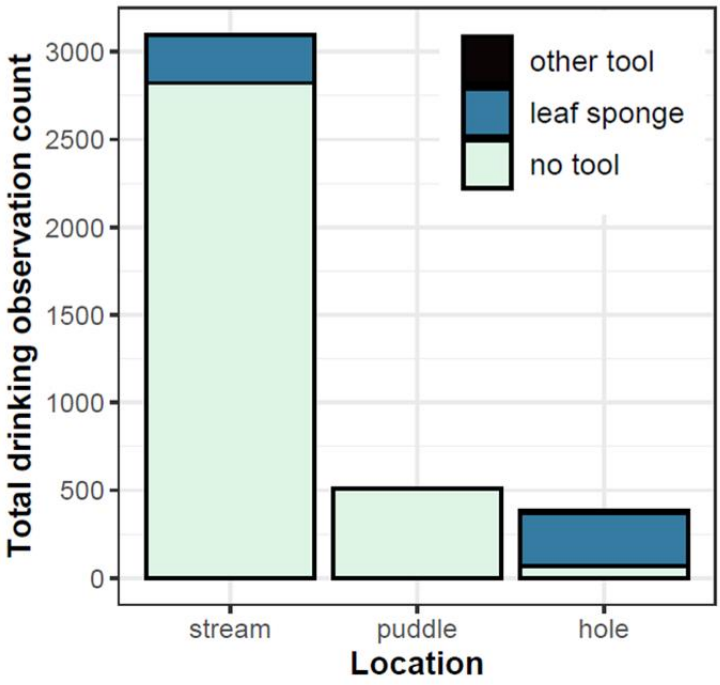
overall rates of drinking, and found chimpanzees in this community most often drink from streams without tools. However, when they do use tools, they preferentially do so to drink at tree holes. Given known age and sex effects on tool use in chimpanzees, we also examined demographic variation in drinking tool use to understand the emergence of this behavior. While females use tools more often than males overall—in part driven by differences in drinking rates at different locations—both males and females use tools more frequently at tree holes than other locations when they do drink there. Finally, comparisons by age indicate that this selectivity strengthens over development with older chimpanzees showing a more pronounced effect of using tools more often at tree holes, suggesting that younger chimpanzees may exhibit exploratory tool-use behavior. These results pinpoint the specific function of tool use during drinking and further suggest that even simple tools may require learning for use in appropriate contexts.

Graphical Abstract



Chimpanzees use tools to access hard to reach water in tree holes.





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Research Highlights

- We examined patterns of wild chimpanzee tool use during drinking to identify the function of this behavior.
- Chimpanzees at Kanyawara use leaf sponges specifically to access water that is out of reach in tree holes.
- Male and female chimpanzees were equally likely to use tools at tree holes, but females were more likely to use drinking tools reflecting increased likelihood of them drinking from tree holes.
- Young chimpanzees were more likely to use drinking tools in broad contexts which became more refined with age

1. Introduction

Unlike humans, chimpanzees are not always obligated to consume water on a daily basis, as they can often obtain water from their food resources (Pontzer et al., 2021; Wrangham, 1977). However, chimpanzees are frequently observed drinking in the wild. Drinking water can serve a variety of purposes, including necessity in times of drought-related stress or other forms of seasonal variation in water or food availability (Nelson et al., 2022; Wessling, Deschner, et al., 2018; Wessling, Kühl, et al., 2018). Chimpanzees are also notable amongst nonhuman animals in that they will sometimes use tools to obtain water—especially a particular type of tool called a leaf-sponge (McGrew, 2013; Van Lawick-Goodall, 1968). When leaf-sponging, a chimpanzee chews leaves to create a wadge and submerges it in water, which the wadge absorbs like a sponge. They put the wadge in their mouth, suck the water out, and then repeat this behavior. Chimpanzees also use other tool-types to obtain water, including leaf spoons where leaves are used to scoop water without first chewing the leaf, leaf-folding where leaves are first folded in the mouth before being dipped into the water, and dipping sticks where sticks are submerged into water and sucked on (Lapuente et al., 2017; Sousa, 2011; Sugiyama, 1995; Tonooka, 2001; Van Lawick-Goodall, 1968). However, leaf sponging is among the most widely documented tool use behaviors across wild chimpanzee field sites. This behavior is even

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sometimes described as a cultural universal across the species range, absent in only one study community. (Whiten et al., 2001).

Although it is clear that leaf-sponges and other tools are used for drinking water across wild chimpanzee communities, the specific function of using tools to obtain water is in fact not clear given that chimpanzees can obtain water without using tools by using their mouth or hands to drink. This stands in contrast to many other forms of toolmaking and tool-use in the wild, where chimpanzees use tools to access specific food resources that they could not otherwise eat without the tool. This is the case for termite- and honey-fishing with sticks, nut cracking with rocks or wooden hammers, and pestle pounding to access palm hearts (Boesch & Boesch-Achermann, 2000; Boesch et al., 2009; Boesch et al., 1994; Hicks et al., 2005; McGrew, 1992; Sanz & Morgan, 2009; Stanford et al., 2000; Whiten et al., 1999; Yamakoshi & Sugiyama, 1995). While leaf-sponges or other drinking tools may play a similar role in accessing a resource (water), this inference is less clear than for some other types of foraging tools, such as nut cracking, because chimpanzees are also capable of drinking water without such tools. Indeed, they are frequently observed using their mouths to drink directly from water sources, or also using their fingers to dip into such sources (Goodall, 1986; Lanjouw, 2002; Quiatt, 2006). In that way, drinking tool-use might parallel honey foraging where tools are used by individuals to obtain a difficult to obtain resource with greater ease. Chimpanzees use tools to obtain honey from nests of stingless bees (*Meliponula* sp.) that are either underground or in fortified tree cavities with cryptic holes, but are less likely to use tools to eat honey from stinging bees (*Apis sp.*) which are conspicuously made in tree cavities and are more accessible by hand or mouth (Boesch et al., 2009; McLennan, 2011, 2015; Sanz & Morgan, 2009; Stanford et al., 2000).

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However, drinking tools also differ from honey tools in that there are no unprotected sources of honey (i.e. puddles of honey). Drinking also differs from other contexts of tool use as there is no substitute for water as a resource compared to other types of food. For example, chimpanzees could choose a non-nut food source rather than using stone tools to crack open nuts.

Testing the function of drinking tools requires examining not only instances of drinking with a tool, like most prior work on this behavior (Matsusaka et al., 2006; Quiatt, 2006; Sousa, 2011; Sugiyama, 1995; Tonooka, 2001), but also instances of drinking without tools. This would allow us to pinpoint the contexts in which chimpanzees specifically use tools as opposed to drinking more generally. Here we test two hypotheses about the potential function of tool-use for drinking water in wild chimpanzees. The *access hypothesis* posits that chimpanzees use tools to access otherwise hard-to-reach water, similar to the function of tools to access other inaccessible resources such as insects, honey, or nuts. This hypothesis is based in part on the observations from the Bossou and Nimba communities in West Africa, where drinking with tools was frequently observed a few days after heavy rains when the forest floor was dry but water remained deep in tree holes that were not accessible by mouth (McGrew, 1977; Sugiyama, 1995). This hypothesis predicts that chimpanzees will be more likely to use tools specifically at inaccessible water sources like tree holes that are not accessible by mouth or hand, compared to accessible sources of water where the water can be directly accessed using the mouth or hands, including ground puddles and streams.

Alternatively, using tools during drinking may be less about access to the water *per se*, but rather because of the bioactive properties of leaves to remove harmful parasites

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from the water before consumption. This *filtering hypothesis* would then be more related to other forms of medicinal plant use which has been observed in wild chimpanzees in other contexts (Huffman, 2001; Krief et al., 2005; Rodriguez & Wrangham, 1993). Given chimpanzees' apparent ability to select plants with bioactive properties (Freymann et al., 2024; Krief et al., 2005; Krief et al., 2006), the filtering hypothesis predicts that chimpanzees are more likely to use tools for drinking at stagnant water sources where harmful pathogens can accumulate compared to running or filtered water (Avery et al., 2008; Galat et al., 2008; Stommel et al., 2016). Specifically, this hypothesis predicts that tool use will be more likely when chimpanzees are drinking from tree holes and puddles (i.e. sources of still water) compared to streams (i.e. flowing water). While both the access and filtering hypotheses predict increased tool use at tree holes, the filtering hypothesis more broadly predicts that tool use should occur more frequently at any sites of stagnant water—e.g., both puddles and tree holes—compared to streams, as tool use would play a similar filtering role at any such source of standing water.

Demographic factors may also affect tool-use in drinking contexts and provide additional insight into its function. First, female chimpanzees across populations use tools more often than males, especially for foraging (Boesch & Boesch, 1984; Byrne, 2007; Gruber et al., 2010; Koops et al., 2015; McGrew, 1979). In the case of drinking tool use specifically, there is evidence for increased need for water by female chimpanzees imposed by the demands of lactation (Nelson et al., 2024; Nelson et al., 2022). This predicts that female chimpanzees might use tools for drinking, and generally drink more, than males. However, no prior work has specifically examined how different sexes choose to use drinking tools at different locations. Second, there is a growing body of evidence that

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chimpanzees socially learn tool-use behavior (Call et al., 2005; Whiten, 2017). Such developmental changes have been especially well-documented in the context of termite fishing (Lonsdorf et al., 2004; Lonsdorf & Sanz, 2022; Musgrave et al., 2021; Sanz & Morgan, 2013), and adults are also more likely to engage in goal-directed rather than exploratory object manipulation compared to young individuals (Lamon et al., 2018). This pattern predicts that adults would be more likely to use tools for drinking overall. However, young chimpanzees also use tools and may sometimes do so more often than adults (Sugiyama, 1995) even in the context of drinking (Matsusaka et al., 2006), so age-related shifts in drinking tool use specifically are currently unclear. Finally, it is important to note that what may differ by individuals could be their overall propensity to drink at all at different kinds of locations. Given that the physical affordances of different locations may then drive differences in the methods used to drink at that location, it is important to consider not only how frequently different age-sex classes use tools to drink, but also *where* they generally choose to drink water at all.

To test between possible functions of tool use during drinking, we use a large dataset spanning 14 years of observation from the Kanyawara community of chimpanzees living in Kibale National Park, comprising specific observations of all-occurrence drinking and tool use. To pinpoint the function of chimpanzee drinking tools, we examined all drinking behavior (with or without tools) to evaluate the context of when chimpanzees are choosing to use a tool—that is, the chimpanzees' propensity to use tools at tree holes, puddles, and streams when they drank at these different key locations. To assess if this pattern changed over the life-course, we further examined how individuals varying by age and sex used tools at different locations. Finally, we examined overall rates of drinking at

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these different locations, again contrasting individuals varying in age and sex, to assess if some aspects of tool use patterns might depend on chimpanzees' choices about where to drink water via any method. Overall, our large set of drinking observations allows us to determine who uses tools to drink as well as the specific contexts in which they do so.

2. Methods

2.1 Study site and community

The chimpanzees of the Kanyawara community live in the northwest sector of Kibale National Park, Uganda, in an area made up of mostly moist medium-altitude evergreen forest with small areas of grassland, swamp, colonizing forest and pine plantation (Chapman & Wrangham, 1993). The Kanyawara chimpanzees have been continuously studied since 1987 by the Kibale Chimpanzee Project (KCP), and individuals have been habituated to human observers since 1992. Overall, the analyzed dataset comprised drinking records from 81 chimpanzees (47 females and 34 males), ranging in age from 0.1 to 63.2 years (mean = 19.6 years), who individually contributed between 1 to 14 years of observations.

2.2 Data collection

At KCP, trained Ugandan field assistants conduct systematic daily data collection that involves entering the forest and following the chimpanzees from the time they wake up in the morning until they make their nightly nests at the end of the day. The field assistants are paired with one individual collecting data on a focal individual and the other individual focusing on group-level data collection which includes scans of all chimpanzees present in the party of the focal individual every 15-minutes. In addition, this field assistant records all observations of drinking noting the identities of the individuals drinking, the

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location of the drinking event as well as the method of water acquisition. Field assistants are also instructed to record all cases of tool use in detail including on a specific tool-use datasheet. When tools are used in drinking, field assistants note the type of tool being used as well as a description of how the tool is being used and if others are observing the tool use. For further details about data collection procedures at KCP, see Emery Thompson (2020).

2.3 Data extraction

For this study, we extracted all occurrences of drinking by Kanyawara chimpanzees from hand-written observation notes from 2005 (when field assistants were specifically instructed to record all drinking behavior) through 2018. A drinking event was defined as any instance where an identified chimpanzee was observed drinking water. For example, if two chimpanzees were observed drinking at a stream, we recorded this as two separate drinking events. Any event where the individuals were not identified was excluded. We coded each drinking event for location and grouped events into three categories: stream, puddle, and tree hole (see Figure 1 for example photographs of chimpanzee drinking behaviors at different locations with or without a tool). Streams included any description of running water. Puddles included any mention of drinking on the ground, pools, wallows, or footprints. Finally, tree holes included holes in the trunks or hollows of trees as well as holes that form in buttress roots. All other locations were coded as 'other' and if a specific location was not noted, we coded this as 'unknown'.

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Figure 1: Examples of wild chimpanzees' drinking methods and locations. (a) Examples of drinking from streams without a tool, using the mouth; (b) Drinking from a tree hole without a tool, by dipping fingers into the crevice. (c) An infant using a leaf sponge to drink from a tree hole. (d) An adult using a leaf sponge to drink from a tree hole. (e) Examples of puddles formed on the ground in animal footprints. (f) Example tree hole and recovered leaf-sponge after it has been gently pulled apart by researcher.

We also coded each event for the use of a tool. All mentions of leaf-sponge, sponge or wadge were coded as 'leaf-sponge'. If chimpanzees used another tool type (a stick or a leaf dipped into water), these were coded as 'other tool use'. When descriptions of drinking did not explicitly mention tool use, we assumed that a tool was not used as the field assistants are trained to note all tool use behavior. We excluded all events where drinking or water consumption was not clear either because the field assistant did not see water on the tool or that individuals were sucking the juice from leaf or fruit wadges. We also excluded one unsuccessful drinking event from analysis where individuals tried to obtain water but did not drink.

2.4 Statistical analyses

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We analyzed data in R (R Development Core Team, 2023). First, we examined all instances of drinking to identify the contexts in which chimpanzees used a tool to drink or not; here, tool use (yes or no) was the dependent variable. To do so, we implemented generalized linear mixed models (GLMMs) using the *glmer* function from the lme4 software package (Bates et al., 2015) with a binomial distribution. The base model included chimpanzees' *identity* (to account for repeated within-subject observations), *year* (as an ordinal factor, to account for any global shifts in behavior due to changes in ecology or data collection protocols), and *month* (as an ordinal factor, to account for any seasonal changes in ecology) as random factors. We further included age *cohort* and *sex* in the base model to account for any differences in baseline likelihood of using tools across individuals (for example it is commonly reported that female chimpanzees engage in more extractive foraging than males). Then in successive models we added *location* of drinking (stream, puddle, or tree hole) as our primary test of the function of tool use. We further added interactions between *location X sex* and *location X cohort*, to test if males and females (or younger and older chimpanzees) differed in where they used tools beyond any global differences in rates. For example, this allowed us to test not only if females used tools more than males, but if their use may have served a different function in terms of where they implemented tool use behaviors. In these analyses, we defined three age cohorts: infants under 5 years, juveniles under 10 years, and older subadult and adult chimpanzees over 10 years. These cutoffs were based on life history transitions in this species (Emery Thompson & Sabbi, 2024), and allowed us to assess potentially non-linear age changes. We compared the fit of different models using likelihood ratio tests (Bolker et al., 2009), and conducted post-hoc tests using the *emmeans* package with a Tukey correction (Lenth, 2024).

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We also analyzed the subset of data comprising chimpanzees aged 5 years and up. We excluded the youngest cohort, infants, because they were likely traveling with their mother, so any tool use in that cohort likely reflected the influence of another individual. This also allowed us to examine age in years as a continuous predictor, to examine more nuanced aspects of developmental change in the subset of older chimpanzees who could make more independent tool use decisions. These analyses used the same sequence of model predictors as in the models using cohort, excepting the exchange of cohorts for the continuous age predictor.

In the final set of models, we then compared overall rate of drinking at different locations (regardless of technique) to assess if there were demographic differences in drinking that might impact tool use decisions. Here, we calculated an annual drinking rate for each individual, by dividing counts of drinking observations by total hours of observational effort for that chimpanzee in the year. We based this calculation of drinking effort on observations as recorded by 15-minute scans, and chimpanzees who had received less than 50 hours of observation were excluded from this analysis. Here, we again focused on the subset of chimpanzees aged 5 years and up who could make more independent decisions, and implemented linear mixed models (LMMs) using the *lmer* function. Base models accounted for chimpanzees' *identity* and *year* as random factors (since these analyses examined annual rates, we could not include month as a predictor). We then added *sex*, *age*, and the interaction between *sex X age* to successive models to test if chimpanzees systematically varied in their overall drinking rates. For these analyses, we analyzed overall drinking rates as well as drinking rates at each of the possible locations (streams, tree holes, and puddles) separately; this allowed us to assess if there were any differences in these

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demographic patterns across locations where chimpanzees could drink. For all statistical analyses, we report the parameter estimates in the electronic supplementary material (ESM).

3. Results

Overall, the complete dataset comprised 4087 drinking events, with 625 involving tool use and the rest without (see Figure 2a). The vast majority of tool use events were leaf-sponging (604 events), with a smaller minority involving other forms of tool use (dipping a stick, leaves, or in one instance bark into water; 21 total events). There were also several distinct locations recorded across the dataset (see Figure 2b): while the majority of drinking occurred at steams (3102 events), other drinking occurred in holes in trees (356) or holes in tree buttresses (26); or from puddles on the ground (299) or from water in animal footprints on the ground (212). Finally, both tool and non-tool drinking events were distributed fairly consistently across this period of 14 years of observation (see Figure 2c).

In analyses of tool use, we focused on instances of drinking where the location of drinking was known (3993 events, 97.7% of the total data), to test our primary hypotheses. In these analyses, we excluded ~2.3% of the data where the location was either not recorded (88 instances) or comprised a rare, unusual location (such as from top of a mushroom; 4 instances), as well as 2 observations where the identity of the drinking chimpanzee was not known. In this dataset, tool use for drinking was observed 596 times, comprising 14.9% of the total set of drinking events. Across events with known locations, chimpanzees drank most often from streams: 77.6% of the observations comprised drinking from streams, 12.8% comprised drinking from puddles, and 9.6% comprised drinking from holes. However, there was also variation in the methods that chimpanzees used to drink at these

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different locations: while tools were used in 81.9% of drinking events at tree holes, they were used only at 9.0% of drinking events at streams and at 0.82% of drinking events at puddles (see Figure 3a for breakdown of drinking with versus without a tool by location).

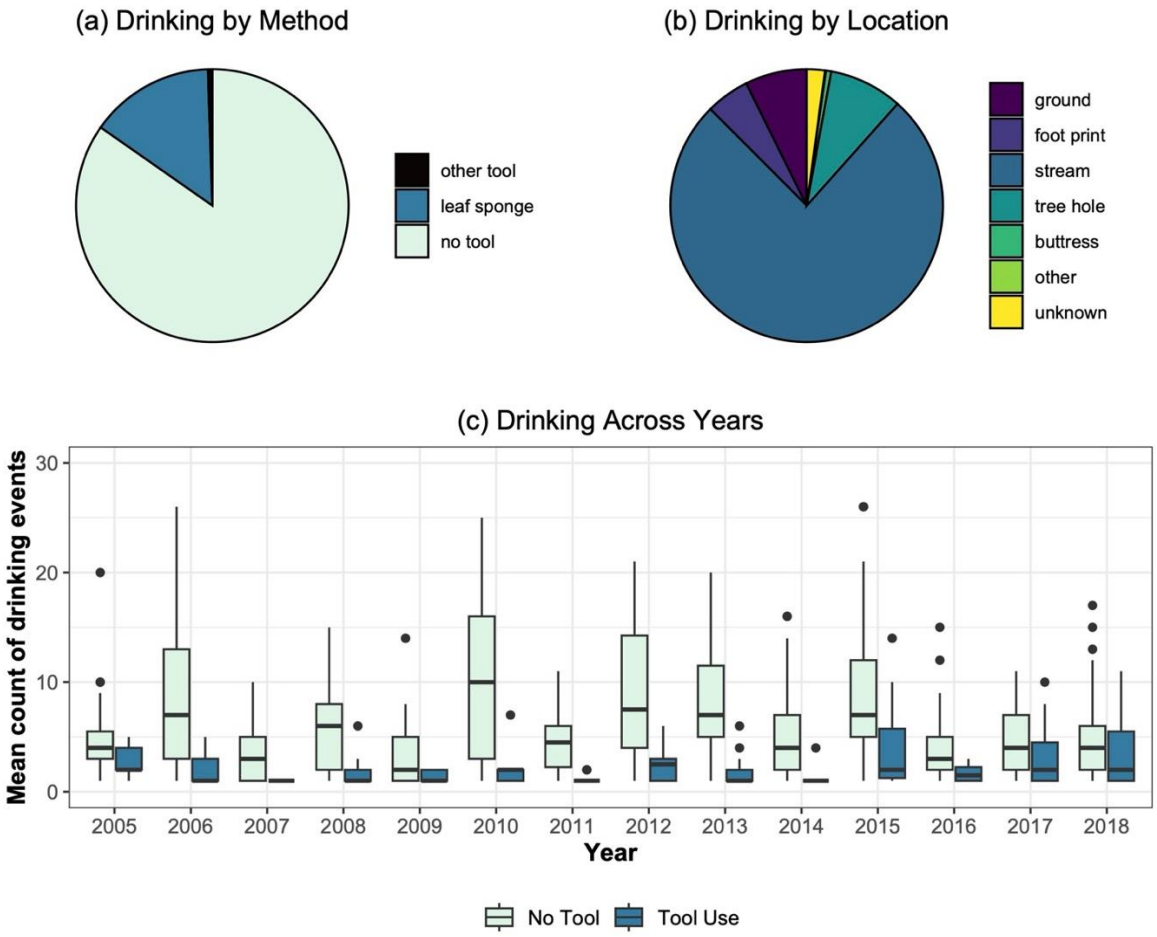

Figure 2: Patterns of drinking in wild chimpanzees. (a) The majority of drinking events did not involve a tool (chimpanzees used either the mouth or their hands), but some instances involved using a leaf-sponge or other tool (dipping a stick or leaves into water). (b) Drinking from *streams* was the most common location, but chimpanzees also drank from the ground and footprints (categorized as *puddles*), or from tree holes or crevices in buttresses (categorized as *holes*). (c) Annual mean drinking counts across individuals across the dataset, split by tool use or non-tool drinking. Boxplot hinges indicate the lower and upper quartiles, lines indicate median counts, whiskers indicate the minimum and maximum range, and outliers are plotted as individual points.

We first used GLMMs to model use of tool versus no tool for drinking, to test whether chimpanzees preferentially used tools to drink water at specific locations. Here,

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inclusion of *location* (in addition to the base model) improved fit [$\chi^2 = 820.43$, df = 2, $p < 0.0001$]; posthoc tests indicated that chimpanzees were much more likely to use tools specially when they drank at tree holes compared to all other locations (both streams and puddles), as well as more likely to use tools at streams compared to ground puddles [$p < 0.0001$ for both cases]. These models also indicated that both quadratic age *cohort* and *sex* (included in the base model) were significant predictors of *overall* tool use as we expected: juveniles and adults were more likely to use tools overall compared to infants [$p < 0.05$ in both cases], and females were overall more likely to use tools than males [$p < 0.005$]. To specifically test whether there were not only demographic differences in overall tool use, but also in patterns of tool use at particular locations, we then included the interactions between *cohort X location* and *sex X location*. In fact, neither interaction term further improved model fit compared to the second model [*cohort X location:* $\chi^2 = 3.02$, df = 4, $p = 0.55$, n.s.; *sex X location*: $\chi^2 = 1.06$, df = 2, $p = 0.59$, n.s.; see electronic supplementary ESM Table S1 for all parameters from this model]. That is, while juveniles and adults were more likely to use tools to drink than infants, and females were more likely than males to use tools, these different age-sex classes did not systematically differ in their likelihood to use tools at the different possible locations when they did drink there. For example, while there were 255 observations of females using tools to drink at tree holes compared to 58 from males, this in part reflected the fact that females were observed drinking from tree holes more often overall (304 events for females versus 78 for males). If males did visit tree holes, however, they used tools at a rate similar to females (females: 83.9% of observations; males: 74.4%; see Figure 3b for model estimates).

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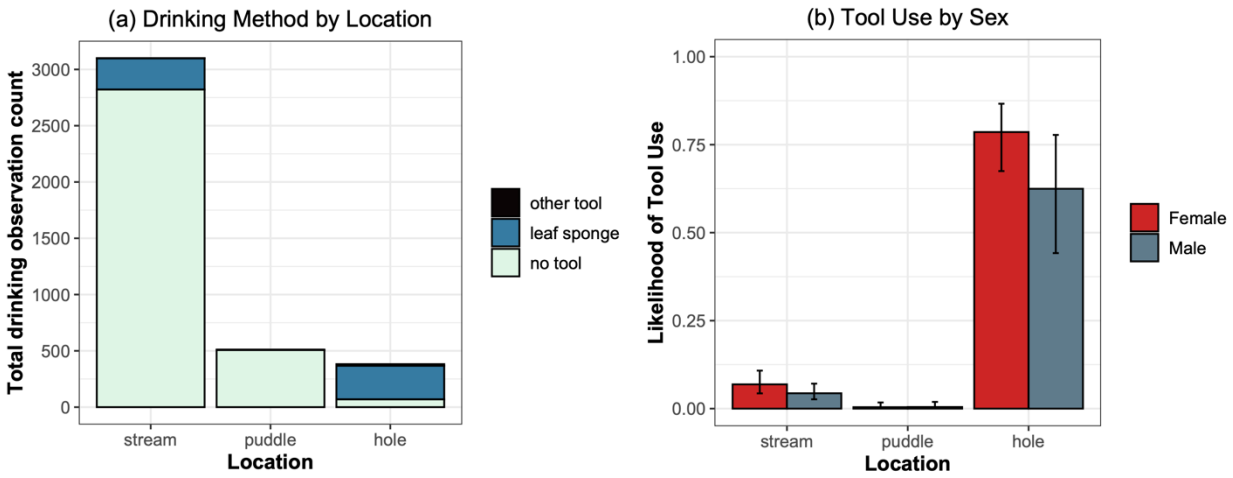

Figure 3: Tool use for drinking across locations. (a) The majority of drinking events occurred at streams, but chimpanzees were more likely to use tools when they did drink at a tree hole. (b) Males and females were similarly likely to use tools in the events where they visited tree holes to drink. Predicted effects are derived from models also accounting for subject's identity, year and month along with location, cohort and sex; error bars indicate 95% confidence intervals.

Given the overall lower rates of tool use in infants (see Figure 4a), and the fact that dependent infants were likely to be traveling to different drinking locations with their mothers, we then examined variation in the sample of chimpanzees ages 5 years and older, who could make more independent decisions, to examine more nuanced developmental trajectories in drinking tool use in this age range using continuous age as a predictor rather than cohorts to capture any changes across the adult lifespan. This subset of the data comprised 3722 drinking events, with 549 involving tool use. As in the full sample, inclusion of *location* to the base model including *age* and *sex* improved fit [$\chi^2 = 745.87$, df = 2, $p < 0.0001$]; posthoc tests indicated the same pattern as in the full sample with the most tool use at holes, followed by streams [$p < 0.0001$ for significant cases]. As with the prior models, *sex* was again a significant main predictor in this model [$p < 0.001$]. We then added the interactions between *location X age* as well as *location X sex*, as in the prior analyses, to examine if individuals varied in their propensity to use tools when they drank

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at a particular location. While the inclusion of *location X sex* again did not improve fit, the inclusion of the interaction between *location X age* did improve model fit [χ^2 = 9.03, df = 2, $p < 0.05$; see ESM Table S2 for all parameters from this model]. Post hoc comparisons of age slopes indicated that tool use at holes increased with age compared to at streams [$p < 0.05$]. That is, while chimpanzees in this age range showed increasing selectivity in *where* they used tools: older chimpanzees used them more often at hole locations, and less often at streams, with a uniformly low rate of tool use at puddles across this range (see Figure 4b). As with the analyses using the full dataset, there was no further improvement by the inclusion of the interaction between *location X sex*, indicating no difference in overall likelihood to use a tool when males versus females did drink at a particular location.

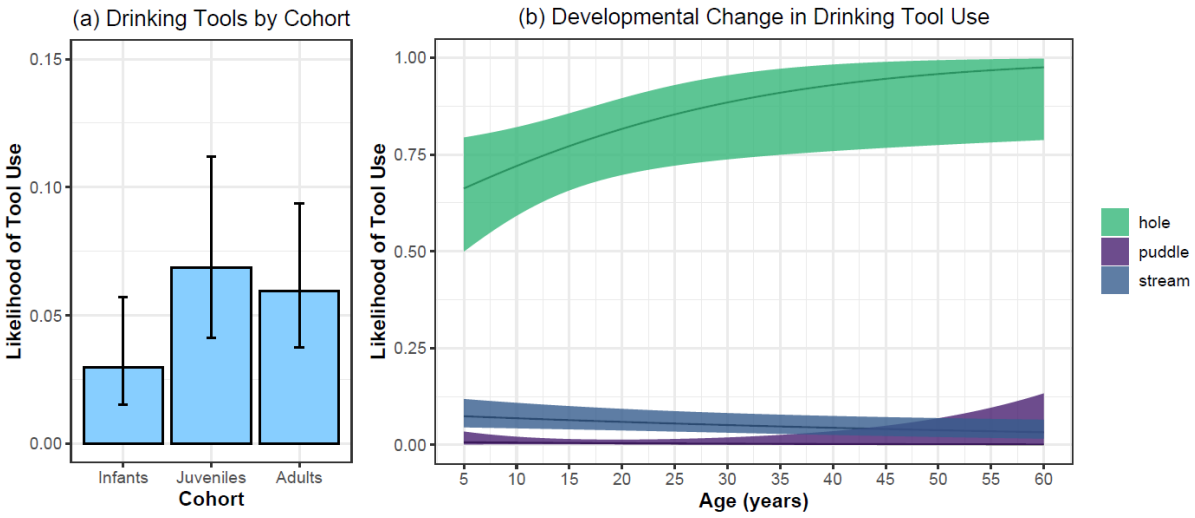

Figure 4: Drinking tool use across the lifespan. (a) Overall drinking tool use rates across age cohorts. Infants were less likely than either juveniles or adults to use tools to drink. Predicted effects derived from models also accounting for subject's identity, year and month, along with location, sex, and cohort; error bars indicate 95% confidence intervals. (b) Drinking tool use rates across different locations in juveniles and adults. Chimpanzees showed age-related change in drinking tool use by location: whereas tool use increased at tree holes with increasing age, it declined at streams. Predicted effects derived from models also accounting for subject's identity,

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year and month, along with location, age, and sex; ribbons indicate 95% confidence intervals.

We finally examined patterns of overall drinking rates, to examine if some chimpanzees selectively drank more or drank more at particular locations. We again focused on the juvenile and adult sample to examine more autonomous choices about where to drink, given that infants generally travel with their mother. As noted previously, to do so we calculated annual drinking rate accounting for the total time that individual chimpanzees were observed, and used linear mixed models to assess variation in rates. Our first analysis examined overall drinking rates (at all locations including unknown locations) to assess basic demographic differences in drinking. Here, inclusion of *age* improved fit [χ^2 = 7131.5, df = 1, p < 0.0001]: older chimpanzees were observed drinking more frequently overall than younger ones. Inclusion of *sex* further improved fit [χ^2 = 8.05, df = 1, p < 0.005; see ESM Table S3 for all parameters from this model]; females drank more often than males. However, there was no further improvement by including the interaction between sex and age [χ^2 = 0.001, df = 1, p 0.98, n.s.]. These patterns likely reflect differential need for water in these different age-sex classes: whereas adult chimpanzees are larger and thus require more water, females likely have greater water needs than males due to pregnancy and lactation.

Breaking this analysis down by location, however, revealed distinct patterns of drinking in different locations that provide more specific insights into tool use decisions. First, drinking at streams mirrored the pattern in the entire sample (see Figure 5a): *age* improved fit [χ^2 = 10.47, df = 1, p < 0.005] such that older chimpanzees drank at streams more frequently than younger ones. In addition, sex further improved fit [χ^2 = 4.59, df = 1, p < 0.05; see ESM Table S4 for all parameters from this model], such that females drank

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at streams more than males; the further inclusion of the *age X sex* interaction again did not improve fit. This pattern is unsurprising given that most drinking events in the entire sample occurred at streams. However, drinking at tree holes showed a different pattern. While drinking rates at tree holes were overall lower than at streams (see Figure 5b), here, the inclusion of the *age X sex* interaction did improve model fit compared to the model with only the main effects [$\chi^2 = 4.31$, df = 1, $p < 0.05$; see ESM Table S5 for all parameters from this model]; posthoc tests indicated that drinking rates at holes overall declined with age, and also declined faster for females than males [$p < 0.05$]. That is, the total rate of drinking at tree holes by any means actually declined with age, especially for females. Finally, there were similarly low rates drinking at puddles, with no differences across chimpanzees by age or sex (see Figure 5c and see ESM Table S6 for all parameters from this model). Overall, these results align with our primary analyses of tool use, and also confirm that even though all chimpanzees were most likely to be observed drinking from streams, female chimpanzees (especially younger females) engaged in relatively more drinking at tree holes than did other age-sex classes.

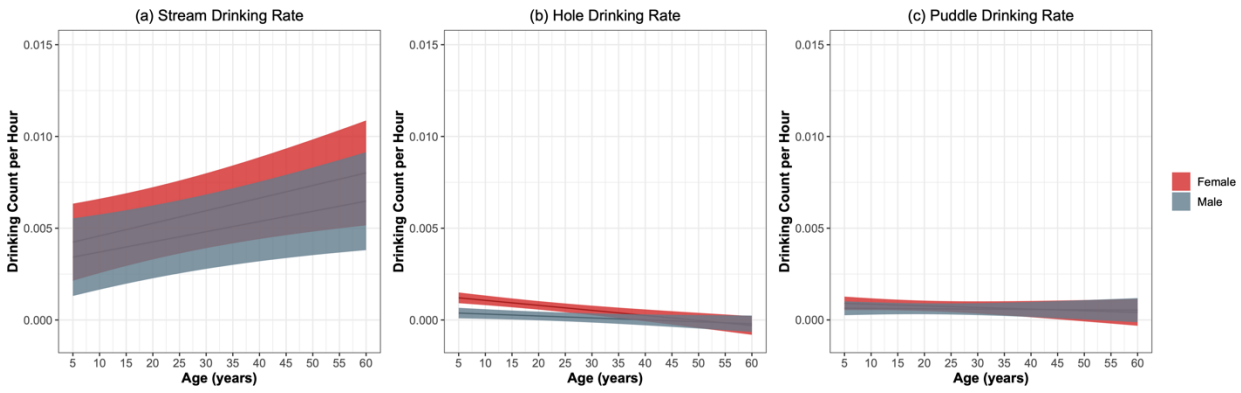

Figure 5: Drinking rates at different locations by juveniles and adults. (a) Chimpanzees drank at streams more often than other locations; overall rate of drinking at streams increased with age, and females were observed drinking more often than males. (b) Overall rate of drinking at tree holes

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declined with age, with a steeper decline in females. (c) Low rates of drinking at puddles were consistent across the lifespan. Predicted effects derived from models also accounting for subject's identity and year, along with age, sex, and their interaction; ribbons indicate 95% confidence intervals. Note that the y-axis range is kept consistent across drinking locations to depict the differences in overall drinking rates at streams versus tree holds and ground puddles.

4. Discussion

To investigate why chimpanzees use tools to drink water, we examined all drinking events with and without tool-use across 14 years of observation to understand the contexts that drive chimpanzees to use such tools. We found that while the vast majority of drinking events occurred at streams where water is flowing and accessible by mouth or hands, Kanyawara chimpanzees were specifically more likely to use *tools* when drinking from tree holes, where water is generally less accessible by mouth compared to streams and puddles. Overall, this pattern of results supports the *access hypothesis*: chimpanzees use tools for drinking when they are unable to reach the water source with their mouth or hand. Conversely, there was no support for the *filtering hypothesis.* While chimpanzees frequently used tools at tree holes which could contain stagnant water, leaf-sponges and other tools were almost never used at puddles—another primary source of stagnant water. Indeed, chimpanzees were actually more likely (both in terms of percentage of events and overall count) to use tools at free-flowing streams than at puddles. We further found that while there were developmental changes and sex differences in both tool use patterns and overall drinking rates, chimpanzees of all sex-age classes used tools more at tree holes than other locations when they did drink there. Overall, this underscores the importance of examining both when chimpanzees use and do not use tools to identify the functions of this behavior.

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Our results are consistent with several previous studies at other wild chimpanzee sites. For example, at Bossou in Guinea, drinking tools were also used to access water from tree holes (Sugiyama, 1995), including in a long-term experimental context where researchers filled tree holes with water to observe tool-use behavior (Sousa, 2011). Similarly, chimpanzees at Budongo in Uganda were more commonly observed using leaves for drinking at tree holes compared to when drinking at rivers or streams (Quiatt, 2006) and the Tongo chimpanzees in Democratic Republic of Congo were observed using moss sponges to drink from tree holes that were not wide enough to directly drink with their mouths (Lanjouw, 2002). Interestingly, the Comoé chimpanzees in Ivory Coast were more likely to use leaf-sponges to drink from tree holes that were wide enough in diameter for the tool and their fingers, but used water dipping sticks to obtain water from narrow tree holes (< 8cm) (Lapuente et al., 2017), which suggests some nuanced sensitivity to the functional properties of these tools. Our results are also consistent with an emerging set of captive experiments showing that great apes will use tools to gain access to out-of-reach fluid rewards. For example, captive chimpanzees have been observed spontaneously making tools to drink hard-to-access fluids, including using branches with chewed, frayed ends that acted as sponges to absorb water (Kitahara-Frisch & Norikoshi, 1982), and will select and use functionally appropriate tools that serve as straws to access juice (Manrique & Call, 2011). More generally, apes seem to have a rich causal understanding of the properties of fluids, including understanding how water can be used as a tool to make other items float into reach (Hanus et al., 2011; Mendes et al., 2007; Tennie et al., 2010). Overall, the results of this study align with a large body of evidence that chimpanzees can use tools to access out-of-reach foods and liquids in foraging contexts.

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In contrast to support for the *access hypothesis*, we did not find support for the specific predictions for the *filtering hypothesis* that chimpanzees were using leaf-sponges to filter pathogens from stagnant water sources based on these analyses. In particular, chimpanzees rarely used tools to drink water from puddles, and in fact, while tool use was most common at tree holes specifically, it was also more likely to occur at flowing streams compared to puddles on the ground (which is opposite the prediction of this hypothesis). However, we should note some potential limitations of this conclusion. One is that we were unable to assess how long water had been standing in tree holes or in puddles on the ground, so it is possible that the increased use of tools at tree holes may reflect that the water inside tree crevices is more stagnant compared to pools that form on the ground after rainfalls. However, several descriptions of chimpanzees drinking from pools of water on the ground specifically noted that the water was stagnant, and most of those events did not involve tools. Another limitation is that field assistants did not systematically record the species of plant used for tools, which could bear on their use for medicinal purposes. However, when it was recorded (in just under 15% of leaf sponging events) chimpanzees were most often observed making leaf-sponges of *Afromomum spp.* and *Uvariopsis congensis*—both species that have been shown to have medicinal properties (Alo et al., 2012; Krief et al., 2006; Okigbo & Ogbonnaya, 2006). Nonetheless, *Afromomum* is also one of the most common leaves in the forest (Chapman et al., 1995) and *U. congensis* is a preferred food of chimpanzees in Kibale National Park (Emery Thompson et al., 2020; Watts et al., 2012). This is consistent with data from Budongo where the species of leaf-sponge was systematically recorded, and also corresponded to commonly available and eaten species (Quiatt, 2006). Consequently, it is plausible that these leaves were chosen because of

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convenience rather than their properties *per se*. As such, future studies should consider the species of the tools used especially in foraging or drinking contexts to further test hypotheses about medicinal plant use.

Another important consideration is variation in tool use as well as drinking patterns across different chimpanzee communities. Although leaf-sponges are by far the most common tool used for drinking at Kanyawara (97.1% of cases of tools used for drinking analyzed in the current study) and at Budongo (Quiatt, 2006), there is variation in drinking tool use across the species' range. The Bossou chimpanzees engage in leaf-folding for the majority of their drinking tool behaviors (Tonooka, 2001) and have also been observed using sticks or leaves to dip or spoon for water (Sugiyama, 1995). In addition, the Comoé and Bossou chimpanzees were more frequently observed using water dipping sticks compared to leaf-sponges (Lapuente et al., 2017; Sugiyama, 1995; Tonooka, 2001). In contrast, chimpanzees at Kanyawara were never observed leaf-folding, and only occasionally were they observed using sticks or leaves to dip or spoon for water. This variation in preference for particular drinking tools could reflect variation in local ecologies or available resources. Alternatively, it may reflect some socially-learned cultural differences across the species range, including overall community specific preferences for particular tool substrates. For example, chimpanzees at Budongo have never been observed using sticks in a foraging contexts and experimentally do not use them in a novel context of honey foraging (Gruber et al., 2009), even though appropriate sticks are certainly available in their forest. This suggests that some variation in tool choices may be dependent on socially-learned skills.

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We also found that while tools were used most often at tree holes, the Kanyawara chimpanzees most often drank from streams. Access to different kinds of sources of water, especially seasonally, varies across wild sites with some sites having limited access to running water throughout the year (Lanjouw, 2002; Lapuente et al., 2017; Pruetz & Bertolani, 2009; Wessling, Deschner, et al., 2018; Wessling, Kühl, et al., 2018). This appears to impact when and how different chimpanzee communities use tools. For example, chimpanzees at Bossou, used tools during months of low rainfall or days after rains when water was no longer available on the ground and only in tree holes. While we controlled for month and year in the current analyses to account for any possible seasonal or ecological variation in drinking observations (such as rainfall), given our primary hypotheses, we did not explicitly test for this kind of seasonal variation in the use of drinking tools. This was outside of the scope of this study because it relies not only on changes in rainfall through the year, but might also be affected by the diet of chimpanzees as particular foods may be more likely to induce drinking as is the case with red colobus monkeys in Zanzibar ingesting salty foods (Nowak, 2008). However, future studies on the use of drinking tools should consider if this tool use is driven by reduced seasonal access to either running water or puddles of fresh water shortly after heavy rains and specifically consider the length of time between drinking events and the last rainfall. This would allow us to understand whether drinking tools were more likely to be used at particular locations if many days have passed since the last rainfall suggesting that the water was more likely to be stagnant. Overall, this suggests that systematic comparisons of drinking behavior across different populations can provide additional insights into the decisions to use these tools.

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One important aspect of the current work is that both males and females were similarly likely to use tools when they visited tree holes compared to other locations. That is, while females (and older chimpanzees) were more likely to use tools to drink water overall, this appears to have been driven primarily by choices about where to drink rather than variation in overall propensity to use tools *per se*. For example, while both males and females predominantly drank from streams, females (and especially younger females) were more likely than males to drink from tree holes. Indeed, we also found that females were more likely to be observed drinking at all, suggesting that females may face a stronger need for water and may address this in part by increasing drinking from less common sources such as tree holes. In line with this, some prior work has found that chimpanzee mothers at Gombe in Tanzania were more likely to drink in the dry season compared to non-mothers, and that low-ranking and mid-ranking mothers were more likely to drink during late lactation compared to early lactation (Nelson et al., 2022). In addition, Gombe females had higher concentrations of urine specific gravity indicating higher levels of dehydration compared to males and the females who were in the middle phase of lactation were more dehydrated than females who were not pregnant or lactating (Nelson et al., 2024), This suggests that the costs incurred from motherhood, such as lactation, necessitate additional water consumption and may motivate females to seek out water compared to other individuals. In addition, while all chimpanzee age-sex classes showed the highest rate of drinking from streams, younger females also showed elevated rates of drinking from tree holes which might reflect a higher overall need for water in line with the differences in overall rates of drinking. Future work at Kanyawara should therefore examine whether females' choice to drink at particular locations, and to use drinking tools when doing so,

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may similarly reflect variation in the need to access additional water sources in different reproductive states.

In terms of development, chimpanzee tool use at tree holes increased with age. However, it should be noted that *drinking rates* at tree holes (which is generally already low) declined with age. That is, the increased use of tools at tree holes with increasing age is driven by increased tool use at these locations and not just drinking at these locations more. This differs from the pattern at streams which is generally more frequent and also increases with age. Notably, chimpanzees at Kanyawara did not only use tools to drink from tree holes: they were sometimes observed using leaf-sponges to drink water from streams, even though they could easily access the water with their mouth or hands at these locations. One possible explanation for tool use at stream concerns the development of these skills. Specifically, our results show that chimpanzees shift in the locations where they use tools as they age: while chimpanzees in general use tools more often at holes, younger chimpanzees show a relatively higher rate of tool-use at streams than adults. That is, chimpanzees seem to become more selective in using tools at tree holes as they mature, such that younger chimpanzees try tools at more varied locations than do older adults. The increasing selectivity in tool use that chimpanzees demonstrate over development may explain some previous reports of drinking with tools. For example, at Bossou, juvenile and adolescent females were observed using tools more than other age-sex classes (Sugiyama, 1995), and a study at Mahale showed that all drinking tool use was by infants and juveniles, and often occurred when the water was easily accessible by hand or mouth (Matsusaka et al., 2006). The prevalence of leaf-sponging in juvenile and adolescent chimpanzees is surprising in that many other documented forms of tool use in wild chimpanzees develop

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over an extended period and may require social learning, often with infants and juveniles learning from their mother as a model. For example, termite fishing requires the acquisition of several intermediate skills and shows a clear developmental improvement (Lonsdorf, 2005; Lonsdorf et al., 2004; Musgrave et al., 2021), and nutcracking shows an even more extended developmental period (Biro et al., 2006; Boesch et al., 2019; Estienne et al., 2019; Hayashi & Inoue-Nakamura, 2011; Inoue-Nakamura & Matsuzawa, 1997). Yet leaf-sponging is distinct from these other forms of foraging-related tool use in two clear respects: it is a fairly simple behavior in terms of its manual actions, and there are also alternative means to accessing the same resource that do not involve tools (e.g. drinking with the mouth or hand). As such, learning *when* such tools for drinking are actually needed (as opposed to *how* to use them) may be the crucial skill that chimpanzees need to acquire.

In this view, younger chimpanzees may experiment more with using drinking tools in contexts where this is not strictly necessary, whereas older chimpanzees tend to do so only when truly needed. In the current results, this is reflected in the analysis of age-related variation in tool use by location, showing that younger chimpanzees showed similar overall tool use rates as older chimpanzees, but also showed more variation in where they used tools: they were less likely to use tools at holes, and more likely to do so at streams, than were older adults. That is, they were somewhat less selective at using tools at holes. This interpretation of the development of chimpanzee drinking tool use might then parallel other documented examples of social learning that concern learning the correct contexts in which to produce a behavior, as opposed to acquiring the mature form of the behavior (e.g., alarm calling in monkeys; (Seyfarth & Cheney, 1986). More generally, emerging theories from developmental psychology suggest the juvenile and adolescent period may be a distinct life

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history stage characterized by more 'exploratory' learning strategies, which adaptively allow younger individuals to appropriately discern the nature of their environments instead of fixating on previously-learned solutions (Gopnik, 2020; Gopnik et al., 2017; Liquin & Gopnik, 2022). In that sense, the greater variation in the locations where younger chimpanzees used tools for drinking may reflect that kind of exploratory behavior. As understanding the development of skills can help pinpoint the psychological mechanisms underlying these behaviors (Lonsdorf & Sanz, 2022), studies of how chimpanzees learn when and how to drink water can provide important insights into the cognitive abilities that shape chimpanzees' interactions in the real world.

In sum, we found support that chimpanzees use tools in the context of drinking primarily to obtain water that would be otherwise out of reach. This function is similar to other foraging tool use such as nut-cracking, ant- or termite-fishing, and pestle pounding for palm hearts (Boesch & Boesch-Achermann, 2000; Boesch et al., 2009; Boesch et al., 1994; Hicks et al., 2005; McGrew, 1992; Sanz & Morgan, 2009; Stanford et al., 2000; Whiten et al., 1999; Yamakoshi & Sugiyama, 1995) where food acquisition would not be possible without a tool. We also found that both male and female chimpanzees were more likely to use a tool at tree holes compared to streams or puddles, such that overall differences in tool use rates reflected overall differences in where males and females chose to drink as opposed to their propensity to use tools when they did drink from a tree hole. Further, young chimpanzees used drinking tools in more diverse contexts than adults, suggesting a potential role for exploratory behavior in drinking tool use acquisition. Overall, these results are consistent with general sex differences and developmental patterns of tool use in wild chimpanzees (Boesch & Boesch, 1984; Byrne, 2007; Gruber et

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al., 2010; Koops et al., 2015; Lonsdorf, 2005; Lonsdorf et al., 2004; Lonsdorf & Sanz, 2022; McGrew, 1979; Musgrave et al., 2021), but also provide a more nuanced explanation as to why these overall patterns may emerge. By examining a context where chimpanzees choose to use or not use a tool, we were able to discern the particular function of the tool, and also provide insight into how chimpanzees learn to use these tools.

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Data Availability Statement

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The data that support the findings of this study will be publicly released in Dryad Data Repository upon publication, and are currently available from the corresponding author upon request.

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