Received: 22 June 2021 | Revised: 8 October 2021 | Accepted: 15 October 2021

DOI: 10.1002/ajp.23342

RESEARCH ARTICLE

AMERICAN JOURNAL OF PRIMATOLOGY WILEY

Tool use behavior in three wild bonobo communities at Kokolopori

Liran Samuni[1,2,3] | David Lemieux[2] | Alicia Lamb[2,4] | Daiane Galdino[2] | Martin Surbeck[1,2,3]

[1]Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA

[2]Kokolopori Bonobo Research Project, Tshuapa, Democratic Republic of the Congo

[3]Department of Primatology, Max Planck Institute of Evolutionary Anthropology, Leipzig, Germany

[4]Department of Biology, Clarkson University, Potsdam, New York, USA

Correspondence

Liran Samuni, Department of Human Evolutionary Biology, Harvard University, 11 Divinity Ave, Cambridge, MA 02138, USA.
Email: liransamuni@gmail.com

Funding information

Max-Planck-Gesellschaft; Harvard University

Abstract

Comparative studies on tool technologies in extant primates, especially in our closest living relatives, offer a window into the evolutionary foundations of tool use in hominins. Whereas chimpanzee tool technology is well studied across populations, the scarcity of described tool technology in wild populations of our other closest living relative, the bonobo, is a mystery. Here we provide a first report of the tool use repertoire of the Kokolopori bonobos and describe in detail the use of leaf-umbrellas during rainfall, with the aim to improve our knowledge of bonobo tool use capacity in the wild. The tool use repertoire of the Kokolopori bonobos was most similar to that of the nearby population of Wamba and comprised eight behaviors, none in a foraging context. Further, over a 6-month period we documented 44 instances of leaf-umbrella use by 22 individuals from three communities, suggesting that this behavior is habitual. Most leaf-umbrella tool users were adult females, and we observed a nonadult using a leaf-umbrella on only a single occasion. While the study and theory of tool technologies is often based on the use of tools in foraging tasks, tool use in bonobos typically occurs in nonforaging contexts across populations. Therefore, incorporating both foraging and nonforaging contexts into our theoretical framework is essential if we wish to advance our understanding of the evolutionary trajectories of tool technology in humans.

KEYWORDS

leaf-umbrella, material culture, *Pan paniscus*, tool technology

1 | INTRODUCTION

The ability to manufacture and use tools was once thought to be a defining feature of *Homo sapiens* (Leakey, 1961), separating us from other animals. However, this notion has been repeatedly challenged, starting with the pioneering work on "termite fishing" in wild chimpanzees by Goodall (1964). Since then, there has been growing evidence of tool use behaviors in various taxonomic groups including mammals, birds, fish, cephalopods, and insects (Van Lawick-Goodall 1971; Mann & Patterson, 2013; Pierce, 1986).

Many of the tool use behaviors documented in nonhuman animals occur in the context of extractive foraging, for example,

Liran Samuni and David Lemieux contributed equally to this study.

bottlenose dolphins (*Tursiops truncatus*) use sponge to protect their beaks while foraging (Smolker et al., 1997), New Caledonian (*Corvus moneduloides*) and Hawaiian (*Corvus hawaiiensis*) crows manufacture hooks to aid prey capture (Hunt, 1996; Rutz et al., 2016) and western chimpanzees (*Pan troglodytes verus*), long-tailed macaques (*Macaca fascicularis*), and various capuchin species (*Cebus spp.*) use rocks as hammers to crack open otherwise inaccessible food (Boesch & Boesch, 1990; Malaivijitnond et al., 2007; Ottoni & Izar, 2008). Although tool use behaviors appear in different taxa, primates remain among the most skilled and prolific tool-users in the animal kingdom. Tool use diversity and complexity is especially evident in chimpanzees (*Pan troglodytes*), one of our closest living relatives, which use tools in a wide variety of contexts such as foraging for food or water, as communicative signals, or for self-maintenance (Boesch & Boesch, 1990; Boesch et al., 2020; Goodall, 1986; McGrew, 2010; Sanz & Morgan, 2013; Whiten et al., 1999). Therefore, the use of tools in chimpanzees is frequently used as a reference to contextualize the origins of human tool technology (Byrne, 2004; McGrew & McGrew, 1992).

In contrast to the prevalence of tool use in chimpanzees, little is known about tool use in our other closest living relative, the bonobo (*Pan paniscus*). Initially, the lack of clear evidence for tool use in bonobos has been attributed to limited observation opportunities compared with chimpanzees (Hohmann & Fruth, 2003; van Schaik et al., 1999). However, with increasing research effort, it appears that bonobos may not be as proficient tool users as would be expected from their genetic proximity to chimpanzees and humans (Furuichi et al., 2015; Gruber & Clay, 2016; Herrmann et al., 2010; Hohmann & Fruth, 2003). To date, the tool use behavioral repertoire of wild bonobos is limited and is mainly described in social, comfort, and hygienic contexts (Furuichi et al., 2015), but they have rarely been observed to rely on tools for extractive foraging tasks. Limited tool use contexts in bonobos and the rarity with which they rely on tools in foraging contexts compared to chimpanzees remains one of the greatest puzzles regarding bonobos' behavior (Furuichi et al., 2015; Koops et al., 2015), especially as both species exhibit similar levels of tool use capacities in captive settings (Gruber et al., 2010). The study of tool use in bonobos and a systematic description of their behavioral repertoire in the wild, in addition to chimpanzees, are therefore a crucial next step to reveal potential drivers contributing to the emergence of tool technologies in hominins (Haslam, 2014; Parker & Gibson, 1979; Washburn, 1960).

When referring to tool use, we adopt the commonly used definition from Beck (1980, p.10): "the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just before use and is responsible for the proper and effective orientation of the tool." To date, 13 different tool use behaviors have been described in wild bonobos, such as drag-branch, leaf-clip, leaf-sponge, and leaf-umbrella (Furuichi et al., 2015; Hohmann & Fruth, 2003; Ingmanson, 1996; Kano, 1982). Whereas some tool-use behaviors like "drag-branch" are observed across bonobo populations (Furuichi et al., 2015, Schamberg et al., 2017), others, like the "leaf-umbrella" have yet only been identified in a single bonobo population at Wamba (Furuichi et al., 2015; Hohmann & Fruth, 2003; Kano, 1982). Here, we present a detailed description concerning the use of leaf-umbrella—the use of leafy twigs as body covers during rain—in an additional bonobo population and across three different communities in Kokolopori. Additionally, we augment the existing behavioral tool use repertoire of bonobos by reporting the absence or presence of previously described tool use behaviors in an additional bonobo population. We then discuss how our findings relate to existing theories on the emergence of tool-use behaviors and how the findings contribute to current debates concerning the discrepancies in tool use behaviors between bonobos and chimpanzees.

2 | METHODS

2.1 | Study site and population

The study was conducted in the Kokolopori Bonobo Reserve (N 0.41716°, E 22.97552°; Surbeck et al., 2017), Democratic Republic of the Congo. The Kokolopori Bonobo Reserve consists predominantly of primary forest with occasional secondary forest and few swampy areas (Surbeck et al., 2017). While systematic research effort and data collection on the occurrence of tool use behavior in Kokolopori bonobos started in 2016, the detailed study of leaf-umbrella tool use observations reported here was conducted between September 2019 and February 2020. Our study population included three fully habituated neighboring bonobo communities (Kokoalongo, Ekalakala, and Fekako), and the community sizes ranged from 9 to 41 individuals at the end of the study period (see Table 1). The three bonobo communities share large areas of their home range and engage in frequent and prolonged intergroup interactions (about 30% of observation days between Ekalakala and Kokoalongo; Cheng et al., 2021; Samuni et al., 2020).

2.2 | Data collection

We conducted full-day party and focal follows (Altmann 1974) of the three bonobo communities daily, performed by a team of trained

TABLE 1 Age class composition of the three bonobo communities during the time of the study

Communities	Adult females	Adult males	Subadults	Juveniles	Infants
Kokoalongo	11	5	2	13	10
Ekalakala	9	3	0	2	4
Fekako	3	4	0	1	1

Note: Age classification was derived from Goodall (1986) and simplified into four categories: infants (0–5 year), juveniles (5–10 year), subadults (10–15 year), and adults (>15 year).

international students and local field assistants. During follows we collected data on the activity, social interactions, and association patterns of the bonobos, using the CyberTracker software (v.3.389–v3.350). Further, we collected ad-libitum behavioral data of tool-use observations and the identity of tool users. Between September 2019 and February 2020, we conducted a systematic study of leaf-umbrella tool use by the bonobos—whenever rain started all observers attempted to identify and document the use of leaf-umbrellas, and when possible, recorded video data (using a Canon Legria HF R806) of this tool use behavior. Due to the *ad-libitum* nature of data collection, we can only provide information on the presence of rather than the rates or absence of tool use occurrences. The observation conditions of leaf-umbrella usage were particularly challenging due to heavy rainfalls, a decrease in light intensity, and because the bonobos typically climbed high in the canopy during these events. Therefore, the number of leaf-umbrella tool use cases presented here are an underestimation of the true occurrence of leaf-umbrella tool use behavior in this population. Whenever possible, we collected, photographed (with scale included), and measured the tools after the bonobos discarded them. We used Adobe Photoshop (version 22.5.0) to calculate the surface area of each measured tool, defined as the total surface area covered by the leaves of the tool. This was quantified as the total pixel count of tool leaves, using the histogram option in Photoshop. We then converted the pixel count to square centimeters using a standardized scale captured in each image (a 10 cm ruler). Finally, we collected daily rainfall data using a rain gauge at the Kokolopori base camp located within the home range of Ekalakala and Kokoalongo. The average annual rainfall between 2016 and 2019 was 2252 ± 96 mm (mean ± *SD*).

2.3 | Ethics statement

The research presented here was noninvasive and adhered to the principles for the ethical treatment of nonhuman primates of the American Society of Primatologists. The research was approved by the Max Planck Society, Harvard University, and the Ministry of Research of the Democratic Republic of the Congo.

3 | RESULTS

Overall, we observed eight out of the 13 different tool use behaviors previously described in wild bonobos at Kokolopori (Table 2). The tool-use behavioral repertoire of the Kokolopori bonobos was most similar to the Wamba population, with a shared 80% (8 out of 10) of the previously described tool use types between the two populations in comparison to 62% (5 out of 8) between Kokolopori and Lomako. We also

TABLE 2 Tool-use behaviors observed in wild bonobos across three populations

Behavior	Description	Study sites		
		Wamba	Lomako	Kokolopori
Play start	Taking object (e.g., leaf, branch, fruit) in hand or mouth while initiating play and during play	+	+	+
Drag branch	Dragging a branch on the ground. Typically, as part of a display	+	+	+
Drop twig	Dropping small branches or twigs from trees after clipping them (presumably to solicit mates)	+	–	+
Aimed throw	Throwing objects, like sticks and fruits, at bonobos and human observers	+	+	+
Leaf-clip mouth	Using mouth to clip leaves in a play context	–	+	–
Leaf-clip fingers	Using fingers to clip leaves to solicit mates	–	+	–
Leaf mouth[a]	Placing a leaf in mouth while swaggering and thrusting to solicit mates	NA	NA	(+)
Leaf-umbrella or rain-hat	Placing detached small branches or twigs over the head/shoulders/back as covers during heavy rain	+	–	+
Leaf cover	Detaching and using small branches or twigs as covers while nesting during heavy rain	+	+	+
Fly-whisk	Using leafy twigs for swatting sweat bees	+	+	+
Leaf-napkin	Using leaves on self to wipe feces/urine	+	–	–
Toothpick	Using a small twig to remove debris from teeth after feeding	+	–	–
Stick scratch	Using a twig or branch to scratch one's own back	+	–	+
Leaf-sponge	Using moss to dip for water accumulated in tree holes	–	+	–

Note: Tool use behavior descriptions and absence/presence of these behaviors for Wamba and Lomako were derived from Furuichi et al. (2015).

[a]First reported in this study—$^{(+)}$the small sample size warrants caution before this behavior can be included as part of the tool-use behavioral repertoire of the Kokolopori bonobos.

observed a tool use behavior previously undescribed in wild bonobos—the use of leaves by a male to solicit for mates by placing the leaf in his mouth while swaggering and thrusting but without clipping the leaf (i.e., *leaf mouth*). However, we only observed this behavior on six different occasions by a single 12 year old male of the Kokoalongo community.

During the 6 months period of detailed leaf-umbrella tool-use observations and data collection (observation days: $n_{Ekalakala} = 121$, $n_{Kokoalongo} = 106$, $n_{Fekako} = 125$), we documented a total of 44 instances of bonobos using leaf-umbrellas during 21 rain sessions. Despite the heavy rain, we were able to capture the majority ($n = 36$, 82%) of detected tool use behavior on video (>3 h of 78 video files). We observed the use of leaf-umbrellas in all three bonobo communities ($n_{Ekalakala} = 23$, $n_{Kokoalongo} = 17$, $n_{Fekako} = 3$, $n_{unknown} = 1$; Table S1) by both males and females, but most tool use instances (70%, $n = 31$) were performed by females. We could identify the tool user in ca. 96% ($n = 42$) of cases and overall, 14 distinct adult females, seven adult males, and one juvenile male were observed using leaf-umbrellas. Across all tool use events, a male and female from Ekalakala (Noir and Violette) were observed using leaf-umbrellas on six different occasions while others were observed only between one and three times (data on leaf-umbrella behavior across individuals is available as Table S1). Although we did not observe any infants (0–5 years) manufacturing and directly using leaf-umbrellas, during rain, mothers typically embraced their infants in a way that offered shelter from the rain, with or without using leaf-umbrella themselves. We could also observe leaf-umbrella tool use during intergroup encounters (10 out of 44 events), defined when individuals from two or more groups were present in the same party.

All the leaf-umbrella tools were manufactured (i.e., sectioned off its original support) from the immediately surrounding canopy vegetation and sometimes even taken directly from the nest. Individuals used their hands to detach branches and then hold them or place them in a horizontal position over their head, neck, shoulders, and/or upper back while sitting in a hunched position (Figure 1 and Video S1), but on three instances the bonobos also placed the covers around their waist onto their thighs. We also observed bonobos pulling branches towards their head without detaching them on three additional occasions. At times, the bonobos readjusted the position and/or orientation of the covers when the covers shifted, potentially because of a decrease in their efficiency. In case the rain persisted (>30 min), some individuals were observed to shake/wring the leafy twigs to presumably remove the accumulation of water and then reused the covers. The actions of tool manufacturing and wringing were bimanual, whereas subsequent adjustments of tool positions were performed using a single hand only.

Out of the 6 months of observation (from September 2019 to February 2020) we observed leaf-umbrella behavior only during 2019—the first 4 months of data collection—corresponding with half the annual rainfall in 2019 (1105 mm; see Figure 2). Out of the 44 tool use behaviors recorded, 20 were observed in October (highest rainfall of the year) and none in January or February when it rarely rained (lowest rainfall in over a year). Individuals were often observed to begin to use leaf-umbrellas as rainfall intensified and used them both when resting in a nest ($n = 3$) or not ($n = 41$). The longest recorded use of a single leaf-umbrella lasted at least 1 h and 30 min by an adult female, but we could not systematically collect data on tool use duration due to environmental conditions. When the bonobos

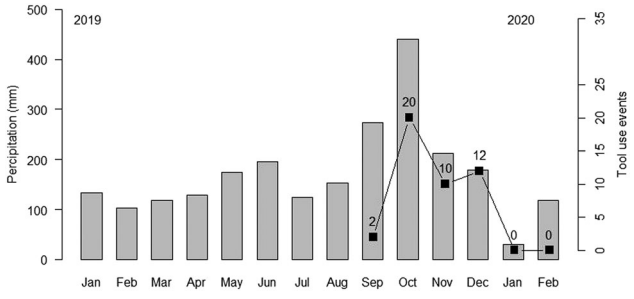

FIGURE 2 Total monthly rainfall (mm, grey bars) and the number of tool use events (black squares) recorded in Kokolopori. Data on rain cover tool use was only systematically recorded between September 2019 and February 2020

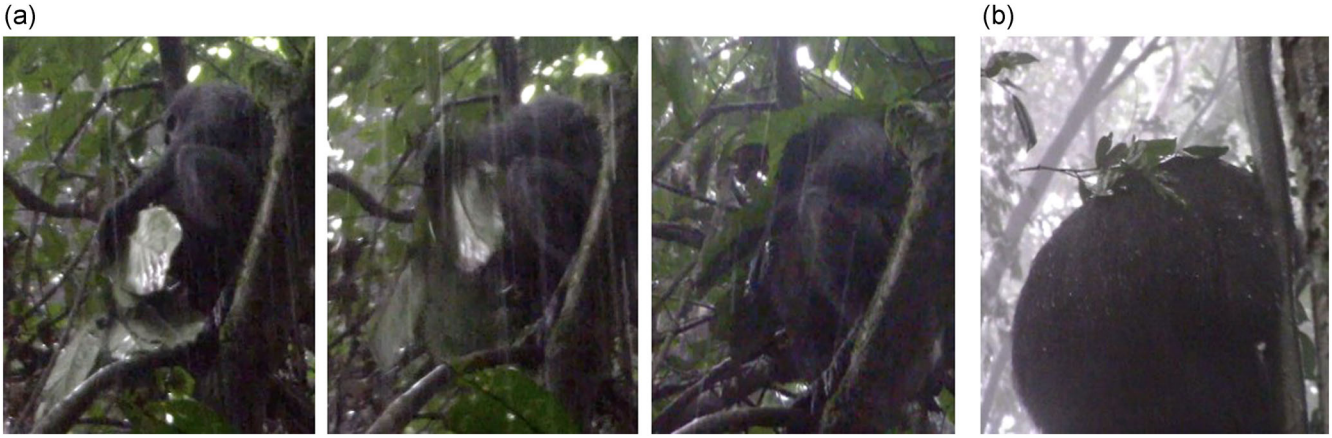

FIGURE 1 Kokolopori bonobos using leafy twigs as covers during heavy rainfall: (a) leaf-umbrella tool-use sequence by an adult female (Simone)—placing the tool over her head and shoulders, (b) leaf-umbrella use by an adult male (Noir)—placing the tool on his upper back and neck

reinitiated travel, after or during rainfall, the individuals observed to use tools typically dropped them before travel. However, in at least one case a female was carrying the leaf-umbrella (the exact tool depicted in Figure 1a) with her while traveling between trees and then reused the cover. Because the tools were often discarded in the canopy and due to the nature of data collection and the challenging observation conditions, we were only able to measure the length of seven leaf-umbrella tools representing six different species (*Cleistanthus mildbraedii*, *Anonidium mannii*, *Greenwayodendron suaveolens*, *Dialium polyanthum*, *Leonardoxa romii*, and *Gilbertiodendron dewevrei*). Tools showed a maximum length of 94 cm and a minimum length of 47 cm (average length = 63 ± 16 cm, see Figure 3). The shape and dimensions of the leaves on the leaf-umbrellas consequently also varied, ranging from 8 × 3 cm up to 35 × 17 cm. The mean surface area of tools was 29 × 29 cm (±12 cm, ranging 15 × 15 cm – 48 × 48 cm).

4 | DISCUSSION

This is the first study to describe the tool use repertoire of a wild bonobo population at the Kokolopori Bonobo Reserve, Democratic Republic of the Congo. Since the initiation of systematic research and data collection in Kokolopori in 2016 we observed eight different tool use behaviors in that population. As expected from spatial distance, the tool use behavioral repertoire of the Kokolopori bonobos was more similar to the Wamba population (ca. 63 km away), than to the population of Lomako (ca. 200 km away). We additionally report the presence of a tool use behavior yet to be described in other bonobo populations—*leaf mouth*—by a single individual. While the report of rare tool use behaviors is notable, the small sample size warrants caution before "leaf mouth" can be included as part of the tool use repertoire of the Kokolopori bonobos. Instead of a novel tool use behavior, "leaf mouth" may represent a variant of "play start" (same action in a different context) or "leaf-clip" (same context with different action) behaviors, but we should note that the latter has never been observed in Kokolopori.

We also provide a detailed description of the use of leaf-umbrellas in this bonobo population. Over a 6-month period, we observed the use of leaf-umbrellas in several adult males and females belonging to three different communities. Individuals displayed this behavior during heavy rainfall by holding or placing a leafy branch over their head, shoulders, and/or upper back while sitting in a hunched position. The regular observation of leaf-umbrella use during the wettest months of the year (Figure 2) could thus represent an adaptation to particular environmental conditions with potential thermoregulatory functions. The tools were extracted from variable tree species, depicting large variation in shape and size of leaves and stalk. Tool properties variation would support the idea that the choice of tool material is opportunistic, especially as individuals were observed using covers of substantially varying sizes, sometimes within the same rain session. Our observations add to previous reports of leaf-umbrella by Kano (1982) at Wamba (located approximately 63 km southwest of Kokolopori) thus reinforcing the idea that this behavior is part of the tool use behavioral repertoire of wild bonobos in a larger area. Variants of this behavior have also been observed in a different context in another bonobo community at Lomako, that is, after the construction of an overnight nest individuals may cover the ventral part of their body with several leafy twigs (Hohmann & Fruth, 2003), thereby suggesting flexibility in the expression of cover tools in bonobos.

According to the behavior prevalence categories defined by Whiten et al. (1999), repeated tool use observations by several individuals are described as habitual. A behavior is often considered as a cultural variant if it is either customary or habitual and found in at least one site but absent in others without relevant ecological explanation (Whiten et al., 1999, 2001). Considering the frequency of this behavior in Kokolopori and that it has only been observed in two study sites (despite observation opportunities in other locations), the use of leaf-umbrellas may be considered as a good candidate for cultural variation in bonobos.

4.1 | Interspecific variation in tool-use

Discrepancies between bonobo and chimpanzee tool use expressions in the wild might be based on differences in the use of tools during extractive foraging (Furuichi et al., 2015), a context with a high observed tool use variability in chimpanzees and a near absence in bonobos except for a single report of female bonobos in Lomako using moss to drink (Hohmann & Fruth, 2003). While the use of tools for extractive foraging tasks is typically more conspicuous and leaves behind traces in the environment that observers can more easily detect and measure (e.g., sticks inside termite mounds or anvils and hammers near cracked nut shells), the use of tools in nonforaging

FIGURE 3 Examples of bonobo leaf-umbrella tools sectioned from (a) *Anonidium mannii*— 94 cm length and 32 × 32 cm surface area, and (b) *Leonardoxa romii*— 47 cm length and 15 × 15 cm surface area. The illustrations are to scale with respect to the proportions of the leaves and stalk

Box 1 Hypotheses of tool use variation across species and populations

- *Limited invention hypothesis*: tool use behaviors are rarely invented and thus mainly rely on social learning, tolerance, and proximity to be maintained (Fox et al., 1999).
- *Demography hypothesis*: larger and interconnected populations have higher chances of developing and maintaining diverse and complex tool kits than smaller and more isolated ones (Henrich, 2004; Shennan, 2001).
- *Opportunity hypothesis*: certain habitats provide more propitious circumstances for tool invention because of repeated exposure to appropriate conditions and materials (Fox et al., 1999).
- *Necessity hypothesis*: energetic benefits promote innovation and the emergence of tool use (Fox et al., 1999).
- *Relative profitability hypothesis*: tool use behaviors are not only a result of ecological or social pressures but are rather just "more profitable than conventional methods" (Furuichi et al., 2015; Rutz & St Clair, 2012).

contexts is expected to be less visible to observers. As such, tool use research and theoretical framework of tool use behavior typically focus on extractive foraging tool tasks (Fox et al., 1999; Gruber et al., 2010; van Schaik et al., 1999). Revealing whether and how bonobos and chimpanzees differ in tool use capacities in nonforaging contexts offers the opportunity to inform theory on the evolution of tool technology and the drivers leading to the acquisition and retention of tool-use behaviors.

Several hypotheses have been developed to explain the discrepancies of tool use within and between species (see Box 1), identifying multiple factors that may contribute to tool use emergence, including ecological opportunities, motor dexterity, cognitive abilities, population size, and social tolerance (Fox et al., 1999; Henrich, 2004; Koops et al., 2014; van Schaik et al., 1999). Hypotheses such as the "limited invention hypothesis" (Fox et al., 1999) or the "demography hypothesis" (Henrich, 2004; Shennan, 2001) emphasize that tolerance or connectedness of a population play a key role in the transmission and retention of tool use. Accordingly, it is surprising that bonobos do not have greater foraging and nonforaging related tool use repertoires compared with chimpanzees, given their assumed increased social tolerance and high rates and prolonged durations of peaceful encounters between groups (Furuichi, 2020; Gruber & Clay, 2016; Koops et al., 2015; Pisor & Surbeck, 2019; Samuni et al., 2020), which offer ample within- and cross-group learning opportunities and a potential basis for more efficient information flow.

The "opportunity hypothesis," posits that repeated exposure to appropriate conditions and materials lead to tool use proliferation. While the use of tools as rain covers is evident in several bonobo and orangutan populations (Fox et al., 1999; Galdikas, 1982; Kano, 1982; MacKinnon,1974; Rijksen, 1978), to date, it has only been observed in one chimpanzee community in the Goualougo Triangle (Sanz & Morgan, 2007). Whereas orangutans also use leaf covers for sun protection (Rijksen, 1978), this behavior has not yet been observed in the more terrestrial bonobos, which rest often on the ground during the hot hours of the day (Samuni & Surbeck, unpublished data). A comparative analysis using meteorological and foliar data would be useful to determine whether shared environmental conditions such as heavy rainfall and availability of certain tool materials (e.g., broader leaves or higher density of leaves that offer greater protection) result in behavioral convergence of rain cover tool use behavior among certain populations of these three species.

The necessity hypothesis identifies the adaptive benefits of tool use in environments of resource scarcity and competitive pressures as the drivers of the evolution of tool technologies (Fox et al., 1999). Accordingly, it has been suggested that bonobos rely less on tools than chimpanzees because the bonobo habitat of the Congo Basin represents a lush environment with higher food availability and lower competition than chimpanzee habitats (Gruber & Clay, 2016; Hohmann & Fruth, 2003; White & Wrangham, 1988, although see Furuichi et al., 2015). However, if resource scarcity would drive the evolution of tool use capacities, whether in a feeding or a nonfeeding context, we would not expect to see bonobos use several nonforaging tool use behaviors but not tool-assisted feeding behaviors. The necessity hypothesis is typically considered in foraging contexts as it posits that energetic needs drive innovation (Fox et al., 1999), with tools used as means to cope with resource scarcity by maximizing nutritional intake. However, energetic gains can also be accrued via a reduction of energy expenditure rather than an increase in energy intake. Therefore, a broader definition of the necessity hypothesis that considers overall energetic balance (Grund et al., 2019) may offer a framework for the emergence of tool use in both foraging and nonforaging contexts. Leaf-umbrellas have previously been suggested as effective means to avoid heat loss during the rainy season (Furuichi et al., 2015; Hohmann & Fruth, 2003; Rijksen, 1978), and in our study the use of leaf-umbrella tools predominantly occurred during the wettest months of the year. If leaf-umbrellas offer thermoregulatory functions of a reduction in energy expenditure during heavy rainfall, then the "necessity hypothesis" offers an explanation for this tool use emergence. Further, the "relative profitability hypothesis" posits that tool use behaviors emerge when they offer a more profitable solution than nontool use methods (Rutz & St Clair, 2012). While the detached leafy twigs did not always appear efficient against the rain (the tool surface area in our study ranged between 15 × 15 cm and 47 × 47 cm), leaf-umbrellas might be more profitable in reducing heat-loss relative to the more conventional method of seeking shelter under an undetached overhanging branch with less direct contact with the individual. Further studies using thermal imaging would be needed to confirm the thermoregulatory functions of leaf-umbrella tool use and whether the "necessity" and/or the "relative profitability" hypotheses may explain the emergence of this tool use behavior across populations.

4.2 | Interindividual variation in tool-use

Several studies in chimpanzee and bonobos suggest a female bias in tool use diversity, frequency, and efficiency, and social learning abilities (Boesch & Boesch, 1984; Boose et al., 2013; Gruber et al., 2010; Herrmann et al., 2010; Lonsdorf, 2005; McGrew, 1979). Similarly, the majority (70%, $n = 31$) of tool users in our study were adult females, and a slightly larger percentage of adult females within our population (59%, $n = 14$) used leaf-umbrella tools than the percentage of adult males (50%, $n = 7$), suggesting potential sex biases in the expression of this behavior. While observations of leaf-umbrella tool use are challenging, there is no reason to expect that the observed sex bias is a result of improved observation opportunities of females in comparison to males, as bonobo males typically rest in lower canopy locations than females (Samuni, personal observation) which allow improved visibility, and as the two unidentified rain-cover users were females. Nonetheless, we suggest that additional research effort is needed to confirm sex biases in leaf-umbrella tool use behavior.

Sex differences in tool use abilities are suggested to already emerge during infancy in wild chimpanzees and might represent a developmental difference shaped by natural selection (Lonsdorf et al., 2004; Lonsdorf, 2005). Studies investigating the development of object manipulation and tool-use flexibility highlight the importance of age in such processes (Inoue-Nakamura & Matsuzawa, 1997; Meulman et al., 2013), and older individuals typically outperform younger ones in both experimental conditions and in the wild (Herrmann et al., 2010; Meulman et al., 2013). In accordance with previous observations of leaf-umbrella usage in bonobos (Kano, 1982), we rarely observed this behavior in nonadults, apart from one juvenile (~8 years). The emergence of tool use competence late during ontogeny may suggest that social learning mechanisms are in place (Meulman et al., 2013). It is however difficult to determine whether juveniles used less tools or whether they simply were more difficult to observe during heavy rainfall. Nonetheless, given the relatively high frequency of leaf-umbrella tool use in bonobos, this context offers the opportunity to investigate the ontogeny of tool use acquisition, and whether exposure to artifacts, tool recycling, and social opportunities impact the acquisition of this behavior.

5 | CONCLUSION

Quantifying behavioral diversity of tool use expressions across bonobo and chimpanzee populations is crucial if we wish to understand the selective pressures that have led to the emergence of tool technologies in hominids. Augmenting the limited data from wild bonobos is of critical importance to address this question. Here, we provide a detailed description of leaf-umbrella tool use in three communities of wild bonobos that add new observations to previous reports of this behavior in this species. As this behavior appears habitual in some populations but not in others, the use of leaf-umbrellas in bonobo might be cultural and offers a context to investigate the emergence of tool use behaviors in wild bonobos across populations, groups, and ontogeny. We also expand on the existing bonobo tool use repertoire described in other sites by reporting whether the same behaviors exist within the Kokolopori population. Given that the behavioral repertoire of the Kokolopori bonobos is most similar to the nearest population of Wamba (Table 2) suggests that potential tool use behavioral traditions in bonobos can be maintained on a large spatial scale.

ACKNOWLEDGMENTS

We thank the Ministry of Scientific Research and Technology in the Democratic Republic of the Congo for the permission to work in country. We also thank the Institut Congolais pour la Conservations de la Nature, the Bonobo Conservation Initiative, and Vie Sauvage, especially Sally Coxe and Albert Lotana Lokasola, for their support of this study in the Kokolopori Bonobo Reserve. We are grateful for the Kokolopori Bonobo Research Project staff members and the people of the villages of Bolamba, Yete, Yomboli, and Yasalakose for granting access to their forest. We are also grateful for Erin Wessling, Kathelijne Koops, and an anonymous reviewer for helpful comments on this manuscript. Funding was provided by Harvard University and the Max Planck Society. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

AUTHOR CONTRIBUTIONS

Liran Samuni: conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); supervision (lead); validation (equal); visualization (equal); writing original draft (lead); writing review and editing (lead). **David Lemieux**: conceptualization (equal); data curation (supporting); investigation (lead); methodology (equal); visualization (equal); writing original draft (lead); writing review and editing (equal). **Alicia Lamb**: data curation (supporting); investigation (equal); writing review and editing (supporting). **Daiane Galdino**: data curation (supporting); investigation (supporting); writing review and editing (supporting). **Martin Surbeck**: conceptualization (equal); funding acquisition (lead); project administration (lead); resources (lead); supervision (lead); writing review and editing (equal).

DATA AVAILABILITY STATEMENT

The data on leaf-umbrella tool use behaviors are available in the supplementary material of this article. Data on other tool use behaviors reported in this study are available from the corresponding author upon reasonable request.

REFERENCES

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3-4), 227–266. https://doi.org/10.1163/156853974X00534

Beck, B. B. (1980). *Animal tool behavior: The use and manufacture of tools by animals*. Garland Press.

Boesch, C., & Boesch, H. (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, *13*(5), 415–440. https://doi.org/10.1016/S0047-2484(84)80055-X

Boesch, C., & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica*, *54*(1-2), 86–99. https://doi.org/10.1159/000156428

Boesch, C., Kalan, A. K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, E. A., Barciela, A., Coupland, C., Egbe, V. E., Eno-Nku, M., Fay, J. M., Fine, D., Hernandez-Aguilar, R. A., Hermans, V., Kadam, P., Kambi, M., Llana, M., Maretti, G., … Kühl, H. S. (2020). Chimpanzee ethnography reveals unexpected cultural diversity. *Nature Human Behaviour*, *4*(9), pp. 910-916. https://doi.org/10.1038/s41562-020-0904-z

Boose, K. J., White, F. J., & Meinelt, A. (2013). Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *American Journal of Primatology*, *75*(9), 917–926. https://doi.org/10.1002/ajp.22155

Byrne, R. W. (2004). The manual skills and cognition that lie behind hominid tool use. In A. E. Russon, & D. R. Begun (Eds.), *The evolution of thought: Evolutionary origins of great ape intelligence* (pp. 31–44). Cambridge University Press. https://doi.org/10.1017/CBO9780511542299.005

Cheng, L., Lucchesi, S., Mundry, R., Samuni, L., Deschner, T., & Surbeck, M. (2021). Variation in aggression rates and urinary cortisol levels indicates intergroup competition in wild bonobos. *Hormones and Behavior*, *128*, 104914. https://doi.org/10.1016/j.yhbeh.2020.104914

Fox, E. A., Sitompul, A. F., & van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orangutans. In S. T. Parker, H. L. Miles, & R. W. Mitchell (Eds.), *The mentality of gorillas and orangutans* (pp. 99–116). Cambridge University Press.

Furuichi, T. (2020). Variation in intergroup relationships among species and among and within local populations of African apes. *International Journal of Primatology*. *22*, 1–21. https://doi.org/10.1007/s10764-020-00134-x

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? *Bonobo Cognition and Behaviour* (pp. 179–214). Brill. https://doi.org/10.1163/9789004304178_010

Galdikas, B. M. (1982). Orang-utan tool-use at Tanjung Puting Reserve, Central Indonesian Borneo (Kalimantan Tengah). *Journal of Human Evolution*. *11*, 1, 19–33. https://doi.org/10.1016/S0047-2484(82)80028-6

Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, *201*(4926), 1264–1266. https://doi.org/10.1038/2011264a0

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Harvard University Press.

Gruber, T., & Clay, Z. (2016). A comparison between bonobos and chimpanzees: A review and update. *Evolutionary Anthropology: Issues, News, and Reviews*, *25*(5), 239–252. https://doi.org/10.1002/evan.21501

Gruber, T., Clay, Z., & Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: Evidence for a female bias in the Pan lineage. *Animal Behavior*, *80*(6), 1023–1033. https://doi.org/10.1016/j.anbehav.2010.09.005

Grund, C., Neumann, C., Zuberbühler, K., & Gruber, T. (2019). Necessity creates opportunities for chimpanzee tool use. *Behavioral Ecology*, *30*(4), 1136–1144. https://doi.org/10.1093/beheco/arz062

Haslam, M. (2014). On the tool use behavior of the bonobo-chimpanzee last common ancestor, and the origins of hominine stone tool use. *American Journal of Primatology*, *76*(10), 910–918. https://doi.org/10.1002/ajp.22284

Henrich, J. (2004). Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses: the Tasmanian case. *American Antiquity*, *69*, 197–214. https://doi.org/10.2307/4128416

Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PLOS One*, *5*(8), e12438. https://doi.org/10.1371/journal.pone.0012438

Hohmann, G., & Fruth, B. (2003). Culture in bonobos? Between-species and within-species variation in behavior. *Current Anthropology*, *44*(4), 563–571. https://doi.org/10.1086/377649

Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, *379*(6562), 249–251. https://doi.org/10.1038/379249a0

Ingmanson, E. J. (1996). Tool-using behavior in wild *Pan paniscus*: Social and ecological considerations. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 190–210). Cambridge University Press.

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*(2), 159–173. https://doi.org/10.1037/0735-7036.111.2.159

Kano, T. (1982). The use of leafy twigs for rain cover by the pygmy chimpanzees of Wamba. *Primates*, *23*(3), 453–457. https://doi.org/10.1007/BF02381327

Koops, K., Furuichi, T., & Hashimoto, C. (2015). Chimpanzees and bonobos differ in intrinsic motivation for tool use. *Scientific Reports*, *5*, 11356. https://doi.org/10.1038/srep11356

Koops, K., Visalberghi, E., & van Schaik, C. P. (2014). The ecology of primate material culture. *Biology Letters*, *10*(11), 20140508. https://doi.org/10.1098/rsbl.2014.0508

Leakey, L. S. B. (1961). *The progress and evolution of man in Africa*. Oxford University Press.

Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, Pan troglodytes schweinfurthii, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*(3), 673–683. https://doi.org/10.1016/j.anbehav.2004.12.014

Lonsdorf, E. V., Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, *428*(6984), 715–716. https://doi.org/10.1038/428715a

MacKinnon, J. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour*. *22*, 1, 3–74. https://doi.org/10.1016/S0003-3472(74)80054-0

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., & Hamada, Y. (2007). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology* *69*(2), 227–233. https://doi.org/10.1002/ajp.20342

Mann, J., & Patterson, E. M. (2013). Tool use by aquatic animals. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *368*(1630), 20120424. https://doi.org/10.1098/rstb.2012.0424

McGrew, W. C. (2010). Chimpanzee technology. *Science*, *328*(5978), 579–580. https://doi.org/10.1126/science.1187921

McGrew, W. C. (1979). Evolutionary implications of sex differences in chimpanzee predations and tool use. In D. A. Hamburg, & E. R. McCown (Eds.), *The great apes* (pp. 441–463). Benjamin Cummings.

McGrew, W. C., & McGrew, W. C. (1992). *Chimpanzee material culture: implications for human evolution*. Cambridge University Press.

Meulman, E. J., Seed, A. M., & Mann, J. (2013). If at first you don't succeed… Studies of ontogeny shed light on the cognitive demands of habitual tool use. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *368*(1630), 20130050. https://doi.org/10.1098/rstb.2013.0050

Ottoni, E. B., & Izar, P. (2008). Capuchin monkey tool use: Overview and implications. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 171–178. https://doi.org/10.1002/evan.20185

Parker, S. T., & Gibson, K. R. (1979). A developmental model for the evolution of language and intelligence in early hominids. *Behavioral*

and Brain Sciences, *2*(3), 367–381. https://doi.org/10.1017/S0140525X0006307X

Pierce Jr, J. D. (1986). A review of tool use in insects. *Florida Entomologist*, *69*(1), 95–104. https://doi.org/10.2307/3494748

Pisor, A. C., & Surbeck, M. (2019). The evolution of intergroup tolerance in nonhuman primates and humans. *Evolutionary Anthropology: Issues, News, and Reviews*, *28*(4), 210–223. https://doi.org/10.1002/evan.21793

Rijksen, H. D. (1978). *A field study on Sumatran orangutans (Pongo pygmaeus abelii, Lesson 1827): Ecology, behaviour, and conservation*. H. Veenman & Zonen.

Rutz, C., Klump, B. C., Komarczyk, L., Leighton, R., Kramer, J., Wischnewski, S., Sugasawa1, S., Morrissey, M. B., James, R., St Clair, J. J. H., Switzer, R. A., & Masuda, B. M. (2016). Discovery of species-wide tool use in the Hawaiian crow. *Nature*, *537*(7620), 403–407. https://doi.org/10.1038/nature19103

Rutz, C., & St Clair, J. J. (2012). The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behavioural Processes*, *89*(2), 153–165. https://doi.org/10.1016/j.beproc.2011.11.005

Samuni, L., Wegdell, F., & Surbeck, M. (2020). Behavioural diversity of bonobo prey preference as a potential cultural trait. *eLife*, *9*, e59191. https://doi.org/10.7554/eLife.59191

Sanz, C. M., & Morgan, D. B. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution*, *52*(4), 420–433. https://doi.org/10.1016/j.jhevol.2006.11.001

Sanz, C. M., & Morgan, D. B. (2013). Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *368*(1630), 20120416. https://doi.org/10.1098/rstb.2012.0416

Schamberg, I., Cheney, D. L., & Seyfarth, R. M. (2017). Bonobos (*Pan paniscus*) perform branch drag displays before long-distance travel. *International Journal of Primatology*, *38*(3), 500–512. https://doi.org/10.1007/s10764-017-9957-x

Shennan, S. (2001). Demography and cultural innovation: A model and its implications for the emergence of modern human culture. *Cambridge archaeological journal*, *11*(1), 5–16. https://doi.org/10.1017/S0959774301000014

Smolker, R., Richards, A., Connor, R., Mann, J., & Berggren, P. (1997). Sponge carrying by dolphins (Delphinidae, Tursiops sp.): A foraging specialization involving tool use? *Ethology*, *103*(6), 454–465. https://doi.org/10.1111/j.1439-0310.1997.tb00160.x

Surbeck, M., Coxe, S., & Lokasola, A. (2017). Lonoa: The establishment of a permanent field site for behavioural research on bonobos in the Kokolopori Bonobo Reserve. *Pan Africa News*, *24*, 13–15. https://doi.org/10.5134/228898

van Schaik, C. P., Deaner, R. O., & Merrill, M. Y. (1999). The conditions for tool use in primates: Implications for the evolution of material culture. *Journal of Human Evolution*, *36*(6), 719–741. https://doi.org/10.1006/jhev.1999.0304

Van Lawick-Goodall, J. (1971). Tool-using in primates and other vertebrates. *Advances in the Study of Behavior*, *3*, 195–249. https://doi.org/10.1016/S0065-3454(08)60157-6

Washburn, S. L. (1960). Tools and human evolution. *Scientific American*, *203*(3), 62–75. https://doi.org/10.1038/scientificamerican0960-62

White, F. J., & Wrangham, R. W. (1988). Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour*, *105*(1-2), 148–164. https://doi.org/10.1163/156853988X00494

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*(6737), 682–685. https://doi.org/10.1038/21415

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R., & Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, *138*(11), 1481–1516. https://doi.org/10.1163/156853901317367717

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Samuni, L., Lemieux, D., Lamb, A., Galdino, D., & Surbeck, M. (2021). Tool use behavior in three wild bonobo communities at Kokolopori. *American Journal of Primatology*, e23342. https://doi.org/10.1002/ajp.23342