Received: 7 July 2016 | Revised: 14 September 2016 | Accepted: 16 September 2016

DOI 10.1002/ajp.22613

RESEARCH ARTICLE

WILEY AMERICAN JOURNAL OF PRIMATOLOGY

Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea

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Funding information

Max Planck Society Innovation Fund; Krekeler Foundation

Wild chimpanzees regularly use tools, made from sticks, leaves, or stone, to find flexible solutions to the ecological challenges of their environment. Nevertheless, some studies suggest strong limitations in the tool-using capabilities of chimpanzees. In this context, we present the discovery of a newly observed tool-use behavior in a population of chimpanzees (*Pan troglodytes verus*) living in the Bakoun Classified Forest, Guinea, where a temporary research site was established for 15 months. Bakoun chimpanzees of every age-sex class were observed to fish for freshwater green algae, *Spirogrya* sp., from rivers, streams, and ponds using long sticks and twigs, ranging from 9 cm up to 4.31 m in length. Using remote camera trap footage from 11 different algae fishing sites within an 85-km^2 study area, we found that algae fishing occurred frequently during the dry season and was non-existent during the rainy season. Chimpanzees were observed algae fishing for as little as 1 min to just over an hour, with an average duration of 9.09 min. We estimate that 364 g of *Spirogyra* algae could be retrieved in this time, based on human trials in the field. Only one other chimpanzee population living in Bossou, Guinea, has been described to customarily scoop algae from the surface of the water using primarily herbaceous tools. Here, we describe the new behavior found at Bakoun and compare it to the algae scooping observed in Bossou chimpanzees and the occasional variant reported in Odzala, Republic of the Congo. As these algae are reported to be high in protein, carbohydrates, and minerals, we hypothesize that chimpanzees are obtaining a nutritional benefit from this seasonally available resource.

KEYWORDS

aquatic foraging, chimpanzee behavior, *Pan troglodytes*, *Papio papio*, tool use

1 | INTRODUCTION

The preservation of tools in the fossil record was once a defining characteristic of archaeological assemblages to recognize remains of *Homo* as distinct from those of *Australopithecus*. However, with the regular discoveries of tool use among living populations of nonhuman primates (hereafter "primates") since the 1960s (Boesch & Boesch, 1981; Goodall, 1964; Nishida, 1973; Shumaker, Walkup, Beck, & Burghardt, 2011), it seems likely that Australopithecines already possessed rudimentary forms of technology (Ambrose, 2001; Wynn, Hernandez-Aguilar, Marchant, & Mcgrew, 2011). Importantly, we can only expect stone tools to ever be preserved in the archaeological record, meaning that other forms of tool use consisting of plant-based materials will be underestimated in these records, and can only be inferred indirectly. To this end, research on primates can illuminate the potential repertoire of tool use behaviors that may reasonably be assumed to have been present in our last common ancestor (McGrew, 2010; Wynn et al., 2011).

The behavioral contexts in which living primates are observed to utilize tools are relevant for hominid evolution, providing insight into the habitat characteristics and motivation that may have driven our ancestors to make use of the first wood and vegetation tools (van Schaik, Deaner, & Merrill, 1999; Wynn et al., 2011). This is particularly evident in the foraging extraction domain, where the majority of primate tool use observed is to gain access to nutritious food resources

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(Bentley-Condit & Smith, 2010; Shumaker et al., 2011). The exploitation of novel food resources via tool use has been hypothesized to have facilitated hominids to support higher energy costs associated with locomotion, living in socially complex groups, and maintaining a large neocortex (Byrne, 1997; Gibson, Gibson, & Ingold, 1994; van Schaik et al., 1999). For example, access to plant underground storage organs (i.e., tubers) and aquatic resources are thought to have provided ancestral hominins with alternative foraging strategies to supplement a hunter-gatherer diet in times of food scarcity (Laden & Wrangham, 2005). Many archaeological sites are uncovered in close proximity to river beds or lake shores, suggesting that access to water was an important aspect of hominin settlements in the dry savanna habitat predominant of the Pliocene (Laden & Wrangham, 2005; Wrangham, Cheney, Seyfarth, & Sarmiento, 2009). However, it remains to be fully understood to what extent these abilities are specific to hominins, or may be part of a shared tool-use repertoire with our closest living relatives, the chimpanzees.

Across primates, we know of at least 20 extant species that incorporate aquatic resources into their diet, but only five species are reported to consume aquatic plants (Kempf, 2009), including the African great apes. Bonobos (*Pan paniscus*) regularly consume water lilies and other aquatic herbs (Uehara, 1990; Wrangham et al., 2009) and gorillas (*Gorilla gorilla gorilla*) inhabit swampy, flooded habitats to feed on terrestrial herbaceous vegetation (THV) that thrives in such wet conditions (Kalan, Madzoké, & Rainey, 2010; Nishihara, 1995). Chimpanzees similarly eat species of THV but have also been reported to consume algae (Kempf, 2009). Algae consumption is rare in primates, and animals in general, other than marine wildlife, nevertheless it is part of the behavioral repertoire of two populations of chimpanzees living in Bossou, near Mt. Nimba, in Guinea and in Odzala National Park in Republic of Congo (Devos, Gatti, & Levréo, 2002; Humle, 2011). The chimpanzees at Bossou are regularly observed to collect algae floating on the surface of water ponds with tools (Humle, Yamakoshi, & Matsuzawa, 2011; Matsuzawa, Yamakoshi, & Humle, 1996). Similarly, "algae scooping" was observed by three male chimpanzees in Odzala, Republic of Congo, but only one individual was seen using a tool made out of a herbaceous stem, whereas the other two males used their hands (Devos et al., 2002). The only other observation of algae harvesting in chimpanzees comes from Mahale, Tanzania, where an adolescent female was once described as using her hands to collect and consume algae (Sakamaki, 1998). Therefore, despite decades of chimpanzee research, there are only a few observations of algae harvesting, suggesting that this behavior is indeed rare.

Alternatively ecological conditions might be such that they do not favor algae consumption in the few long-term chimpanzee research groups that have been studied thoroughly. Additionally, some tool use behaviors, similar to other socially learned behaviors, have been shown to exhibit cultural variation among chimpanzee populations (Boesch, 2012; Whiten et al., 1999). As the majority of chimpanzee populations remains poorly known to researchers and exist in isolated forests or fragments, we are undoubtedly underestimating the true range of chimpanzee behavioral diversity that exists (Boesch, 2012). Therefore we initiated the Pan African Project: the Cultured Chimpanzee (hereafter "PanAf") where we systematically studied chimpanzee populations that are little or unknown across their range in Africa, setting up temporary research sites to collect standardized data using non-invasive methods (Vaidyanathan, 2011). Our aim with the PanAf was thus to contribute to a fuller understanding of the extent of chimpanzee behavioral variation and flexibility. We have already begun to document new behaviors that we observed as a result of the PanAf efforts, such as chimpanzee accumulative stone throwing (Kühl et al., 2016). Here, we report a newly discovered behavioral variant we term "algae fishing" that has been found in wild chimpanzees living in Bakoun, Guinea, a PanAf temporary research site (TRS). We report details with regards to the behavioral techniques observed, a description of the tools used and the type of algae being targeted as well as potential benefits of this behavior. In particular, we noted the hand individuals used to hold the tool while fishing and the material and size of the fishing rods for comparison with the long-term data collected on algae scooping at Bossou, Guinea.

2 | METHODS

2.1 | Study site

All observations were collected at the PanAf TRS located in Bakoun, Guinea (Latitude: 11.9, Longitude: −12.5). The study site is a region just south-west from the classified forest of Bakoun in the prefecture of Tougé, nested within the Fouta Djallon highlands. The Bakoun is a confluent of the large Bafing River running north into the Senegal River in Mali. The environment is dry and windy at the site, with a prolonged dry season from September to April and a rainy season from May to October. The mountainous landscape is characterized by a mosaic of dense tropical and gallery forests found primarily along the rivers and valleys, interspersed with woodland savanna and dry savanna plateaus and a few rocky outcrops.

2.2 | Data collection

The data collection area of the Bakoun TRS was 85 km^2. Chimpanzees have never been studied here before and remain unhabituated to humans. The behavioral data reported in this paper come solely from non-invasive observations and were approved by the Ministère de l'Environnement et des Eaux et Forêts in Guinea as well as the Ethical Committee of the Max Planck Society in Germany. All methods for this study adhered to the legal requirements of Guinea and the American Society of Primatologists' Principles for the Ethical Treatment of Nonhuman Primates.

Remote video camera traps (Bushnell Trophy Cams) were set to record continuously from January 2014 to May 2015. The cameras are triggered autonomously when they detect movement and are set to record for 1 min. They resume recording within seconds if movement continues after each minute of filming. All 1-min video clips where chimpanzees were observed algae fishing were analyzed to extract detailed information about the tool-use behavior of all individuals recorded. The main advantage of remote camera traps is that they require no human presence, and observations can be recorded with minimal disturbance to the chimpanzees. Within the PanAf project protocol, videos are set up within a systematic grid and placed at locations where we have indirect evidence of chimpanzee tool use, namely by finding tool remnants. The first videos of algae fishing were filmed opportunistically in early April 2014, after which more cameras were placed at strategic locations where algae were present. The flooding of the river during the heavy rains forced cameras to be removed from some locations in August 2014, but they were reinstalled when the water level went down in November 2014. Algae fishing tools found during the study period were also collected to measure the length, thickness and weight in the field.

2.3 | Algae fishing events

We defined an "algae fishing event" as all consecutive video clips captured at the same location where chimpanzees were observed to algae fish. As camera traps only record for 1 min and have a variable time delay between sequential videos, we were unable to observe algae fishing events uninterrupted. Therefore, consecutive algae fishing clips recorded within 15 min of one another, and at the same location, were coded as belonging to the same algae fishing event. For each algae fishing event, we recorded the date, time, and location. Within each algae fishing event recorded, we tried to identify individual chimpanzees by considering morphological features of the individual, its fishing position, and its tool characteristics. To estimate the duration of an individual's fishing session, we then summed up the time we saw that individual fishing, assuming they continued fishing during the time delays of the camera, as long as the same individual was algae fishing in sequential clips. We also noted whether individuals used the right or left hand while algae fishing. We remained on the conservative side by attributing identity only to individuals whose features were clear enough to avoid potential confusion, and therefore we tended to underestimate fishing duration. In addition, many individuals could not be identified even within a single event, especially for the younger age classes, juvenile, and infants, and were therefore considered as different individuals. This also leads to an underestimation in fishing duration but also an overestimation in the number of individuals. Due to these various difficulties in identification of individuals across events, we coded "individual algae fishing sessions" observed within an algae fishing event and report the total number of individual algae fishing sessions observed for each age and sex class.

3 | RESULTS

Of the 27,940 video clips recorded at Bakoun during the study period, 1,473 of these contained chimpanzees, and from these, 486 videos showed chimpanzees algae fishing. The chimpanzee algae fishing videos were recorded at 11 different sites distributed across the landscape and included rivers, ponds, and streams. The clips constituted 130 unique algae fishing events where the number of fishing events captured at each algae fishing site ranged from 2 to 32.

Algae fishing events were concentrated during the dry season (Figure 1), and were frequently observed on parts of the river where the algae had the most suitable conditions to grow. During the hot dry season, algae fishing was at its peak and chimpanzees were observed to revisit sites for many days in a row. The algae were filamentous, benthic freshwater green algae of the genus *Spirogyra*, of which 400 species exist worldwide (Tipnee, Ramaraj, & Unpaprom, 2015). The strands are long and characteristically non-branching, and the algae

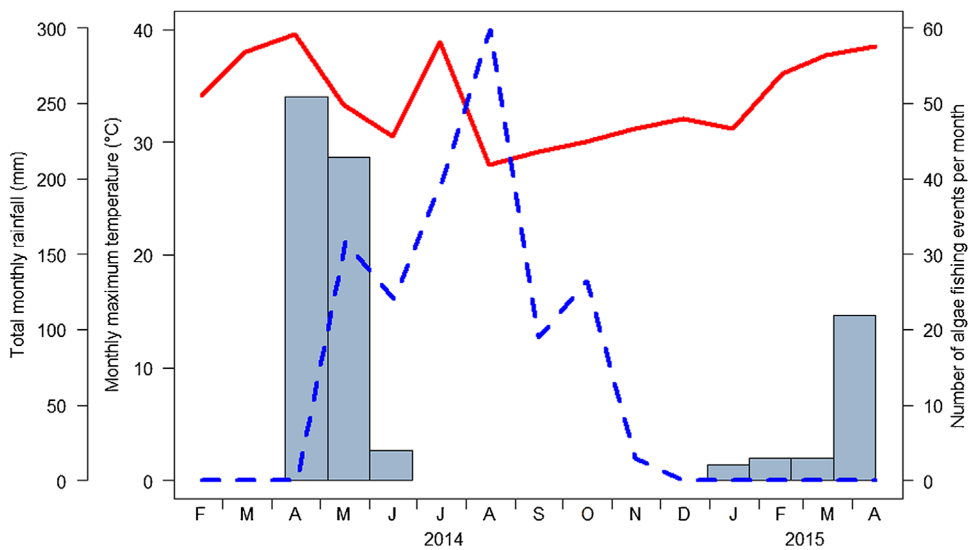

FIGURE 1 Monthly frequency of algae fishing events captured on camera traps versus climatic data. Monthly maximum temperature (red line) and total monthly rainfall (dashed blue line) are plotted alongside the number of algae fishing events recorded per month (gray bars). Importantly, camera traps were set up at targeted algae fishing sites in April 2014 once the behavior had been discovered and some cameras had to be temporarily removed in August–October 2014 due to flooding of the river

are colloquially referred to as "mermaid's tresses" or "water silk." *Spirogyra* grows particularly well in open sunlight and slightly deep, calm freshwater as a charophyte, meaning it grows from the river sediment up into the water (Tipnee et al., 2015). The chimpanzees were observed to fish for algae at sites where the algae occurred in large accumulations at the bottom of the river bed. We rarely observed free floating, surface algae being targeted, as the algae at Bakoun appeared to wash away downstream with the current with the heavy rainfall.

We observed all age and sex classes perform and succeed in fishing for algae from deep ponds or river shores (Supplementary Videos S1–3). Chimpanzees were never recorded to collect any algae directly with their fingers but instead always used a tool to do so. This was true even for 2–3-year-old infants that could already fish with some efficiency. All chimpanzees were observed to hold the tool in one hand by its end, dip it into the water until it seemingly rubbed against the bottom substrate of the water source, and then guide and swivel the tool to enroll long fibers of the algae onto the tool's other end (Figure 2). Following this, individuals removed the sticks from the water and proceeded to bring the tool close to their mouths, close to the end where algae had collected, and then pulled the entire length of the algae on the tool sideward through their lips and thereby transferring the accumulated algae from the stick to their mouths (Figure 2; see also Supplementary Videos S1–3). The hand used for algae fishing was largely consistent within an event, with individuals of all age-sex classes observed grasping the tool with either the right or left hand (Table 1). In only five fishing events, did we observe a juvenile switch hands briefly. Generally, right-handedness was more common but there was variation in handedness among the age-sex classes. Juveniles and infants were mostly using their right hand to algae fish, whereas left-handedness was more frequently observed in older individuals (Table 1). At least seven unique adult males could be identified algae fishing (four out of seven right-handed) and at least four unique adult females (two out of four right-handed), and two adolescent males (one right-handed) and one adolescent female (right-handed). No distinguishing marks could be used to estimate the number of unique juveniles and infants with real certainty, but at minimum, we observed three juveniles (two right-handed) and two infants (both right-handed) algae fishing simultaneously.

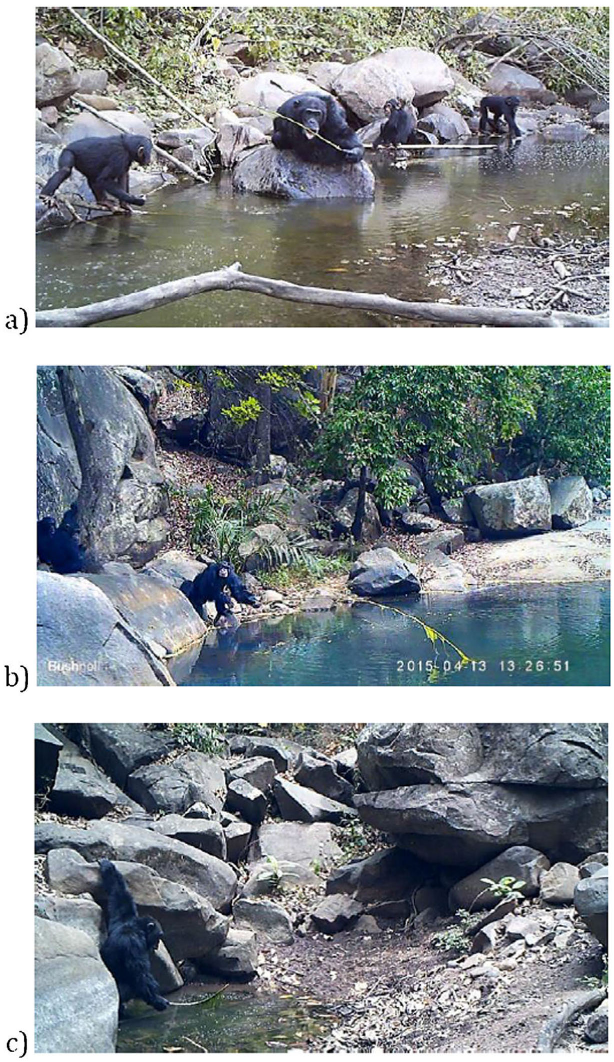

FIGURE 2 Screenshots of algae fishing filmed at three different locations (a, b, and c) in Bakoun, Guinea

Individuals varied in their degree of water immersion while algae fishing. Although chimpanzees generally avoided entering the water while algae fishing, at times we observed individuals to have one or both legs up to the ankle underwater ($N = 24$) or even all four limbs in the water ($N = 5$). With respect to the arms, sometimes the fishing arm was underwater up to the elbow ($N = 11$), but more frequently just the hand was immersed ($N = 68$). We also observed Guinea baboons (*Papio papio*) collecting and consuming algae, albeit using their hands only, and even co-feeding alongside chimpanzees in three out of six baboon algae fishing events recorded opportunistically on the camera traps (see Supplementary Video S2). We know of only one other primate, the black and white colobus monkey (*Colobus guereza occidentalis*), that has been reported to feed with its hands on algae in the swampy forest clearings of the Republic of Congo (Devos et al., 2002).

TABLE 1 Summary of algae fishing performance of chimpanzees by age and sex class

	Individual algae fishing sessions	Proportion right handed	Mean duration in minutes (range)
Adult male	117	0.66	8.50 (1.08–48.02)
Adult female	60	0.43	9.98 (1.25–58.00)
Adolescent male	25	0.20	5.89 (1.42–12.75)
Adolescent female	22	0.91	5.63 (1.42–13.00)
Juvenile	70	0.83	12.57 (1.33–60.58)
Infant	57	0.84	5.58 (1.08–30.17)
Overall average		0.67	9.09 (1.08–60.58)

Handedness and duration was coded for all individuals that could be identified and followed within a single algae fishing event (individual algae fishing sessions). Calculation of the mean duration of algae fishing only included instances where individuals fished for more than 1 min ($N = 189$ individual algae fishing sessions).

TABLE 2 Dimensions of hooked versus smooth algae fishing tools found in Bakoun, Guinea

	Length (cm)	Thickness (mm)	Weight (g)
Hooked ($N = 154$)	68.68 (11–183)	5.84 (2–26)	30.24 (3–368)
Smooth ($N = 455$)	76.23 (9–431)	6.76 (1–30)	36.50 (2–401)

The mean is given with the minimum and maximum of the range shown in brackets.

Trials were made by A.A. and C.B. on site, using a chimpanzee tool that had been left behind on the river shore, whereby 400 g of algae could be collected while fishing for 10 min using the technique seen performed by the chimpanzees. Within a given algae fishing event, individuals were observed to fish for over 1 h at the same spot (see Table 1); therefore a large amount of algae could be consumed during the peak algae fishing season, representing a substantial component to the Bakoun chimpanzee's diet.

Similar to previous descriptions of algae scooping behavior in Bossou chimpanzees, we distinguished between smooth and hooked tools although the majority of the tools we found were smooth (75%; Table 2). Hooked tools were curved, or had barbs or hooked ends, whereas smooth tools were sturdier and more straight. All tools collected were made out of woody branches except for one which was a long bamboo stem (Figure 3). Modifications observed of the tools included stripping smaller branches off the tool (24%), as well as fraying one (27%) or both ends (6%) of the tools using teeth and fingers. Smooth algae fishing tools were significantly longer (Mann–Whitney *U*-test: $U = 30{,}202$, $N_{smooth} = 455$, $N_{hooked} = 154$, $P = 0.01$), thicker ($U = 28{,}391$, $P = 0.0004$), and heavier ($U = 29{,}262$, $P = 0.002$) compared to hooked tools found at algae fishing sites (Table 2). Chimpanzees were observed in the video footage to arrive with tools in hand ($N = 75$ individual algae fishing sessions summed across events; 21%), to re-use tools at the site ($N = 100$; 28%), and to make new tools ($N = 74$; 21%), whereas in all other cases, individuals were already engaged in algae fishing when the camera was triggered so no information was available on the origin of the tool.

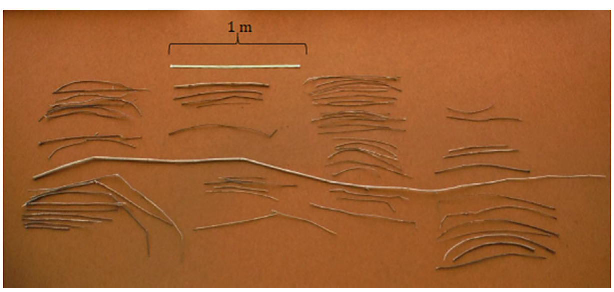

FIGURE 3 Photograph of chimpanzee algae fishing tools collected at 11 algae fishing locations in Bakoun. The center tool is made from bamboo, whereas all others shown are from trees or woody shrubs. Few tools were hooked at the end (e.g., second column from left, just above the center tool), whereas the majority of tools were smooth (see also Table 2)

4 | DISCUSSION

We were surprised to find a population of chimpanzees exhibiting high rates of algae fishing with wooden tools as long as 4 m in length. Although algae fishing only occurred during the dry season, it does occur at high rates and chimpanzees were observed to spend hours fishing. Alternatively, baboons were seen to eat the algae without tools; therefore, we might ask why do chimpanzees use tools to do so? The parts of the river most productive in algae were also quite deep, as seen in Figure 2b and Supplementary Video S1. This would require chimpanzees to immerse themselves deep into the water if they did not use tools, also with some risk due to the very slippery stones in the riverbed. Tools may therefore allow prolonged algae fishing at these sites, permitting access and thereby increasing the efficiency of Bakoun chimpanzees to gather and consume algae, allowing for an expansion of their dietary breadth. Macroalgae, such as *Spirogyra*, are known to be rich in protein, carbohydrate, and lipid content and are also eaten by many human societies as food and medicine throughout Asia (Becker, 2007; Tipnee et al., 2015). For example, humans living in northeast Thailand consume *Spirogyra varians*, locally known as "Tao," who are known to fish the algae from small ponds using bamboo sticks, much in the same manner as the Bakoun chimpanzees were found to do (Tipnee et al., 2015). In fact, the longest fishing rod found at Bakoun was made from bamboo (Figure 3). *S. varians* has a mean content of 16.7% protein, 55.7% carbohydrates, and 18.1% lipids dry matter (Tipnee et al., 2015). The algae are also rich in chlorophyll and phenolic acids, which are valued for their antioxidant properties, and also contain minerals, particularly calcium, magnesium, iron, and some zinc and copper (Tipnee et al., 2015). Due to their highly nutritious properties, macroalgae are commonly sold in health food stores around the world as a vitamin supplement (Becker, 2007). It is therefore not surprising that chimpanzees may be fulfilling substantial dietary requirements by ingesting large amounts of *Spirogyra* algae during the dry season.

It has been suggested that behavioral adaptations used by savanna chimpanzees to manage heat stress could potentially illuminate behavioral strategies that may have been used by ancestral hominins living in similar dry habitats (Wynn et al., 2011). For example, chimpanzees living in the hot savannas of Fongoli, Senegal, are observed to take rests during midday in caves and to bathe in water to help cool down (Pruetz & Bertolani, 2009). The latter observation was all the more surprising given the presumed hydrophobic nature of chimpanzees (Goodall, 1986). However, it appears that many primate species live in close contact with water and quite easily will make use of water for communicative, aquatic foraging, and thermoregulatory behaviors even though they normally appear to avoid getting wet (Kempf, 2009). Chimpanzees therefore are not an exception and in dry habitats especially, such as those found in Senegal and Guinea, it is perhaps crucial for chimpanzees to include more water-based activities into their behavioral repertoire (Pruetz & Bertolani, 2009). The exploitation of aquatic resources during the dry seasons, like the algae fishing described here, may be more similar to what has been proposed for plant underground storage organs in hominin evolution (Laden & Wrangham, 2005). However, the *Spirogyra* algae likely represent a highly preferred and nutritious food source but their consumption is limited by seasonal access, as the heavy rains wash away the algae completely. Hence, we suggest that in Bakoun, tool use permits a more efficient access to a rarely available but highly preferred resource, such as algae, that permits chimpanzees to flourish in an environment otherwise more limited in food and water. It is therefore probable that our last common ancestor would have similarly made and used tools to also engage in rudimentary fishing, to collect and consume rich aquatic fauna, and perhaps flora too.

Similar to chimpanzee accumulative stone throwing (Kühl et al., 2016), we have only observed habitual algae consumption with the aid of tools in west African chimpanzees, *Pan troglodytes verus*, and thus far it appears to be restricted to populations living in Guinea. During the finalization of this paper, we found evidence of algae fishing at two other PanAf TRS in Guinea, one approximately 25 km north of Bakoun, and the other 250 km west of Bakoun. Camera trap footage and additional data are now being collected here as well. Interestingly, even within Guinea, we observe important differences between the algae scooping described at Bossou (Humle et al., 2011) and the algae fishing described here. However, as over 400 different species of *Spirogyra* algae have been described (Tipnee et al., 2015), it may well be that the species floating on the surface in Bossou is a different species than the benthic *Spirogyra* algae targeted in Bakoun. This could explain why Bakoun chimpanzees appear to scrape the bottom of the riverbed to gather the algae with their tools, whereas at Bossou, chimpanzees use tools to gather *Spirogyra* algae floating on the surface of the water. Similarly, hooked tools would be more helpful when collecting floating algae and indeed, at Bossou, they use primarily hooked tools, whereas to collect algae from the bottom of the river, Bakoun chimpanzees use predominantly smooth and more robust woody twigs and branches. There is also a clear size difference, with Bossou tools being on average shorter (56.4 ± 15.0 cm, range: 25–105 cm) than those used by chimpanzees at Bakoun (Table 2), although the thickness of the tools used for algae harvesting at Bossou (6.9 ± 4.1 mm: range 3–32 mm) and Bakoun (Table 2) seems similar. These tool differences could also reflect the different ecology of the algae gathered by both populations. However, despite these differences, we did observe an overall preference for right-handed algae fishing at Bakoun (Table 1) which is similar to the bias for right-handedness observed across all tool use behaviors at Bossou (Humle & Matsuzawa, 2009). Population level bias for right-handedness has been mostly found in captive groups (Humle & Matsuzawa, 2009), therefore algae fishing behavior could provide valuable insight into the development of laterality and handedness in primates within a natural tool using context; however, longitudinal data of individual chimpanzees are needed before these questions can be investigated fully.

The tool-use skills chimpanzees exhibit while harvesting algae show the same level of technological dexterity as they have shown in other contexts, principally by making tools regularly, making them of a size appropriate for the tasks, and transporting tools if necessary and using them in an efficient way (Boesch, 2012; Van Lawick-Goodall, 1970). This demonstrates the flexibility in their technical skills and how this helps them to obtain access to valuable resources in a drier habitat and new context. Such technological skills have been suggested to be present in our human ancestors when they invaded drier, savanna habitat during the course of human evolution (Boesch, 2012). The communality of skills in both species suggests that even with basic technical skills, our ancestors would have been able to adapt and survive in new environmental conditions.

Finally, we would like to stress here that our knowledge of chimpanzees is strongly limited by the number of populations that are known to science. It is striking that new chimpanzee populations studied can still reveal new facets of their abilities (Boesch, 2012; Kühl et al., 2016). It is therefore critical that we concentrate on studying the remaining wild chimpanzee populations if we want to fully understand what is unique in our human skill set.

ACKNOWLEDGMENTS

We would like to express our gratitude to the Max Planck Society Innovation Fund and the Krekeler Foundation for providing generous funding of the PanAf project. We thank the Ministère de l'Environnement et des Eaux et Forêts in Guinea for their permission to conduct research in Bakoun. We greatly acknowledge the hard work of all of our field assistants, especially Keita Konde, Fanta Miguerite, Mamodou Kote, and Djoumou Lasana. We would also like to thank the supporting staff of the Wild Chimpanzee Foundation in Guinea.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Boesch C, Kalan AK, Agbor A, et al. Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea. *Am J Primatol*. 2017;79: e22613. https://doi.org/10.1002/ajp.22613