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Indirect evidence of tool-assisted hunting in the Bantan chimpanzee (*Pan troglodytes verus*) community in southeastern Senegal savanna-woodlands

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ABSTRACT

Chimpanzees use tools extensively, but tool-assisted hunting has been reported at only two sites thus far. Systematic tool-assisted hunting has only been recorded at the Fongoli site in Senegal, where hundreds of cases have been recorded of chimpanzees using tools to hunt bushbaby (*Galago senegalensis*) prey. Here, we report a putative case of tool-assisted hunting at the Bantan study site in southeastern Senegal, based on indirect evidence of tools and tool-making traces in a context similar to that observed at neighboring Fongoli chimpanzee community. If our interpretations are correct, the simplest explanation is that Fongoli females have dispersed to this neighboring community, bringing with them the behavior of tool-assisted hunting. However, the persistence and frequency of tool-assisted hunting at other sites in Senegal is still unknown. Tool-assisted hunting in the Bantan chimpanzee community would present only the third such known site for such behavior among wild chimpanzees thus far.

Keywords: tool-use, chimpanzees, hunting, savanna, Senegal

INTRODUCTION

The use of tools by non-human animals sheds light on their cognitive abilities (Seed & Byrne 2010) and propensity for material culture (Whiten *et al.* 1999; van Schaik *et al.* 2003). Chimpanzees (*Pan troglodytes*) are particularly prolific tool-users that are adept at manufacturing and using tools to obtain food. Chimpanzees commonly use tools to extract invertebrate prey from otherwise inaccessible locations (e.g., “termite fishing” and “ant dipping”: Goodall 1964; McGrew 1974). One chimpanzee community—the Fongoli community of Senegal—commonly hunts mammalian prey with the aid of tools (Pruetz & Bertolani 2007; Pruetz *et al.* 2015), though chimpanzees of Mahale, Tanzania (M-group) have also been reported to hunt a squirrel and hyrax with tools (Huffman & Kalunde 1993; Nakamura & Itoh 2008). Tool-assisted hunting in a non-human primate is particularly relevant to paleo-anthropology because tool-use and hunting have long been considered as critical developments during human evolution (Hill 1982). Additionally, this type of hunting is significant to understanding the evolution of hunting in early hominids, as bipedal apes were likely less adept at hunting prey such as monkeys, the main vertebrate prey of chimpanzees inhabiting forested environments (Pickering & Domínguez-Rodrigo 2012). Although hunting with tools is characteristic of the Fongoli group, it is unknown whether neighboring chimpanzee communities also engage in this behavior. Evidence that nearby chimpanzee groups hunt with tools could provide insight into the scope of behavioral continuity between chimpanzee

populations and may help to better understand the spread of socially-learned traditions in non-human primates. It may also be germane to parsing out the environmental pressures that gave rise to this unusual behavior observed at Fongoli.

Tool-assisted hunting bouts at Fongoli generally occur through a systematic process during which chimpanzees 1) locate a potential *Galago senegalensis* nest cavity in the hollow of a tree trunk or branch, 2) locate a branch to suitably jab into the cavity, 3) modify the branch by stripping it and/or trimming the ends, and 4) jabbing it repeatedly into the cavity to rouse its prey from the nest or injure it, whereupon it is captured by hand and eaten (Pruetz & Bertolani 2007). While this behavior remains rare outside of Fongoli, similar reports have been recorded at Mahale, in which chimpanzees were found to extract mammalian prey from tree and rock dens with sticks for consumption (Huffman & Kalunde 1993; Nakamura & Itoh 2008).

Tool-assisted hunting has been recorded more than 500 times at Fongoli (Pruetz unpublished data). Most chimpanzees at Fongoli, excluding young infants, have been observed to hunt with tools, and females do so relatively more frequently than males (Pruetz *et al.* 2015). Individuals appear to improve in their success with practice, suggesting some degree of observational learning. Most tool-assisted hunting at Fongoli occurs during the wet season from June to September, with some cases also occurring in the transitional months of May and October. The seasonality of tool-assisted hunting, in addition to the patterned tool modification and implementation process,

suggests that this is a regular foraging technique within the Fongoli community, rather than isolated, trial-and-error events.

Here, we present the first putative evidence of tool-assisted hunting of mammalian prey among unhabituated chimpanzees, the Bantan community, which neighbors the Fongoli group. We discuss the implications of this for understanding the spread of socially-learned traditions among chimpanzees and the scope of tool-use in primates more generally.

METHODS

Study Site and Subjects

The Bantan site lies adjacent to and northwest of the Fongoli community in southeastern Senegal, approximately 17 km north/northwest of the town of Kedougou, at 12°45.06325N, -12°15.425983W. This is a savanna mosaic habitat, including woodland, grassland, gallery forest and bamboo woodland habitat types (Pruetz *et al.* 2002).

The Bantan chimpanzee community is an unhabituated group that has been sporadically studied via indirect observational methods since 2000. There are estimated to be approximately 20 individuals in the group, based on nesting data collected in previous studies (Pruetz unpublished data; Micheletti 2018). Ndiaye and students have been conducting research on this community since 2016 (Ndiaye *et al.* 2018; Diallo 2019).

Data Collection

The focus during the study, lasting from May through August 2017, was to survey for signs of chimpanzees in this area and to assess any anthropogenic threats to them (Micheletti 2018). Sixteen reconnaissance walks were conducted to find evidence of chimpanzee's presence. Reconnaissance walks consist of surveying by foot in a predetermined direction along a path of least resistance,

which can deviate by any degree through the survey area (Kühl *et al.* 2008). Additionally, we systematically surveyed forested habitats (e.g., gallery forest and woodland stream areas) where nests and other signs of chimpanzees were thought to be most concentrated. Any evidence of tool-use was recorded, along with the GPS location, the habitat type it was found in, and the type of tool. Tools were brought back to camp, laid flat, and measured from tip to tip.

RESULTS

Two hunting tools were identified by a resemblance to those used by Fongoli chimpanzees in terms of their deposit location, patterns of use-wear, patterns of modification in tool creation, size, and shape (Figure 1).

Hunting tools were sticks found in association with freshly removed leaves and twigs and were situated in the vicinity of possible *Galago* nesting cavities. Both hunting tools were found near each other in a woodland habitat and are from the species *Cordyla pinnata* (Figure 1; Micheletti 2018). Woodland habitats are common locations of tool-assisted hunting by Fongoli chimpanzees, where *Pterocarpus erinaceus* and *Terminalia* sp. trees are common and where *Galago* nesting cavities are frequently located (Pruetz unpublished data). The first tool was discovered under an *Anogeissus leiocarpus* tree, near the trunk, with a diameter at breast height of 33.4 cm and a visible cavity that may have been used by galagos. The second tool was found about five meters away on a termite mound, which showed no signs of recent termite-fishing behavior. The second tool was found in close proximity to the *Anogeissus* tree crown, similar to what is seen at the Fongoli site when 'spear' tools are discarded. All hunting, termite fishing, and ant dipping tools were found in the eastern side of the Bantan community's range based on 2017 nesting data (Micheletti 2018). Furthermore, the

hunting tools were found on June 22, which is considered the wet season, and when most tool-assisted hunting practices are observed at Fongoli (Pruetz *et al.* 2015).

These tools were within the range of Fongoli hunting tool size, which average 10.1 mm in width at midpoint of the tool ($n = 223$ tools) and 64.6 cm in length ($n = 298$ tools), being noticeably longer, thicker, and straighter than termite and ant dipping tools, which are on average less than 5 mm in width (Pruetz unpublished data). Both putative hunting tools ($n = 2$; tool 1 = 83.1 cm, tool 2 = 113.9 cm, $sd=31.8$) fell within the range of tool lengths recorded for the Fongoli community (40–120 cm; Pruetz & Bertolani 2007). The tools showed sites of detachment damage indicated by areas of stripped bark, consistent with side branches being pulled off, as is commonly observed in hunting tools made by Fongoli

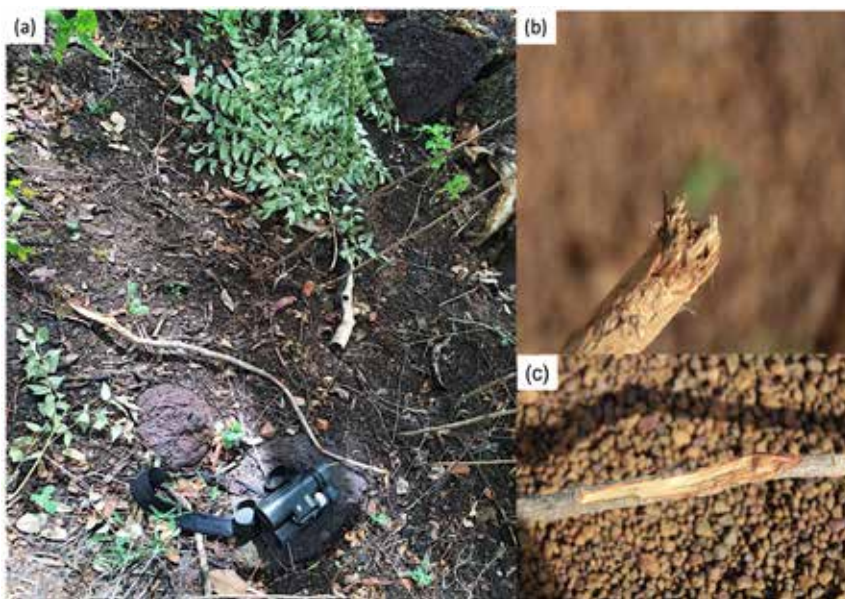


Figure 1. Putative hunting tool in situ with trimmed branches (green leaves in top of photo) and binoculars for scale (a); end of tool with wear pattern (b); and scar on the edge of the tool, typical of removal of side branches and leaves (c). Scar is ~13 cm in length. Photo (a) by J.D.P and photos (b) and (c) by K.N.M.

chimpanzees (Figure 1; Pruett & Bertolani 2007).

DISCUSSION

We report finding modified sticks within the range of the Bantan chimpanzee community in Senegal, interpreted as putative chimpanzee hunting tools. As such, our study extends the record for the rare tool-assisted hunting behavior and contributes to the growing field of primate archaeology (Haslam *et al.* 2009; Haslam *et al.* 2017) that strives to find links between the material culture of non-human primates and their behavior. Our interpretations on the function of the purported tools are based on multiple similarities to known hunting tools of the adjacent Fongoli chimpanzee community. As at Fongoli, these modified sticks were found near potential *Galago* nesting sites, they are within the size range of Fongoli hunting tools and exhibited similar modification and use-wear patterns (Pruett & Bertolani 2007). It is unlikely that the putative hunting tools were made by Fongoli chimpanzees given the location of the site, northwest of the Fongoli chimpanzee core range.

This form of tool-use could be carried between chimpanzee communities through dispersal and could be widespread in Senegal. Adolescent females may spread this behavior between communities upon dispersal, given that at Fongoli, females hunt with tools relatively more frequently than males (Pruett & Bertolani 2007; Pruett *et al.* 2015). It is probable that females from the Fongoli community brought this behavior to the neighboring Bantan community, or vice versa.

Continued research on their tool technology can help to answer questions regarding chimpanzee tool-use, socially-learned traditions, and learning processes. Such transfer of knowledge may provide insights into primate learning processes.

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First observation of fellatio by a wild non-estrus adult female chimpanzee on an adult male, and subsequent meat sharing in Mahale

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ABSTRACT

Sociosexual behaviors such as mounting and genital touch have been extensively reported in chimpanzees. However, there are a small number of reported cases of fellatio, with only a few cases between captive juveniles or adult males. In this study, fellatio from a non-estrus adult female to an adult male holding bushpig meat were observed for the first time. After a series of sociosexual behaviors including fellatio, the meat was shared through begging behavior from the female to the male, suggesting that the series of displayed sociosexual behaviors may have occurred to reduce tension, so that the female could then make a smooth transition to begging behaviors. In addition, the fact that fellatio displayed between male and female in a context similar to previously reported cases of fellatio between adult males suggests that the social bond-strengthening effect of fellatio can also function between an adult male and female.

Keywords: *Pan troglodytes schweinfurthii*, Mahale Mountains National Park, sociosexual behaviors, fellatio, meat sharing

INTRODUCTION

In primates, sociosexual behaviors without mating have been observed in both opposite-sex and same-sex partners. Some of these examples include mounting without penile penetration in the olive baboon (*Papio anubis*) (Owens 1976) and in the Japanese macaque (*Macaca fuscata*) (Takahata 1982), and anal penetration between males in the Geoffroy's spider monkey (*Ateles geoffroyi*) (Busia *et al.* 2018) and in the snub-nosed monkey (*Rhinopithecus roxellana*) (Fang *et al.* 2018).

Although the forms and frequencies of sociosexual behaviors may vary among taxa, they appear to serve social functions. Such behaviors can appear in a variety of contexts, such as mating practices (the Japanese macaque: Gunst *et al.* 2013), negotiation of dominance relations (the snub-nosed monkey: Huang *et al.* 2017), and reducing social tension after aggression or during food sharing (the bonobo [*Pan paniscus*]: de Waal 1990; Hohmann & Fruth, 2000).

Although chimpanzees (*Pan troglodytes*) engage in sociosexual behavior less frequently than bonobos (Woods & Hare 2011; Gruber & Clay 2016), it has been extensively reported (Crawford 1942; Kutsukake & Castles 2004; also see a review by Sandel & Reddy 2021). The frequently reported behavioral types in chimpanzees are mounting and touching of genitals (including mutual touching). However, there are few reported cases of fellatio, or mouthing of the male penis by another individual. Some acts of fellatio are directed to still immature males as reported by Malick & Savage (1977) and Savage-Rumbaugh & Wilkerson (1978) who noted oral-genital contacts among captive juvenile chimpanzees in the con-

text of play. Nishida (1981) reported that an adult female at Mahale mouthed her weaning male offspring's penis as means of appeasing his frustration. Only two reported cases of fellatio were performed on adult males, and both were by other males to reduce tension, one among captive chimpanzees in Primate Foundation of Arizona in the USA (Shefferly & Fritz 1992) and the other among sanctuary-living chimpanzees in Chimfunshi Wildlife Orphanage in Zambia (Brooker *et al.* 2020). To the best of my knowledge, there have been no reports of fellatio by an adult female chimpanzee on an adult male.

This study reports the first such case and describes other accompanying sociosexual behaviors, the context, and subsequent meat sharing.

METHODS

This case was observed between chimpanzees of the M group in the Mahale Mountains National Park, Tanzania, on September 20, 2019 (see Nakamura *et al.* 2015 for details of the study site). The case was recorded first on a field note and subsequently with a video camera (Panasonic HC-W585M). An adult male named Darwin (DW) and an adult female named Fawn (FW) were the participants in this event. FW had borne an infant that year and thus was non-estrus.

OBSERVATIONS

At 08:35 h on September 20, 2019, a large party of the M-group chimpanzees ranged southeast of the area called K1, less than 1 km from the researchers' camp, and DW was followed. At 08:53 h, DW was holding a fresh carcass of a bushpig (*Potamochoerus larvatus*) piglet. At

08:54 h, after climbing a nearby tree, he started eating meat from the bushpig. At 08:58 h, FW with the infant attached to her belly appeared from an unknown location, climbed the same tree, and sat on a lower branch in front of DW. No other individuals were observed in the vicinity. Because a clear view of the subjects was not possible, at 08:58 h the observation location was changed and video recording begun at 09:01 h (Video 1 available online at <http://mahale.main.jp/PAN/2021/005.html>; hereinafter, times in descriptions from video footage are given in hours:minutes:seconds).

At 09:02:04 h, FW touched the erect penis of DW with her left hand for 3 s. Her face was not visible as her back was turned to the camera, but judging from the direction of the head, it is assumed that her gaze was not on DW's penis but on his hand holding the piglet. DW continued to eat without any significant reaction. At 09:02:07 h, FW mouthed DW's penis for 3 s (Figure 1). She touched DW's penis again for 3 s, this time pinching it with her left thumb and index finger. At 09:02:22 h, FW presented her rump to DW and pressed her non-swollen sexual skin against DW's erect penis for 4 s (Figure 2). No penile penetration occurred. FW reached toward DW's hand holding the piglet at 09:02:27 h, but he moved it away from her. At 09:02:31 h, DW turned his back completely on FW. Then, at 09:02:40 h, FW moved to face DW, and at 09:02:51 h, she reached for his mouth and hand holding the meat while peering into his face. At 09:03:22 h, FW loosely grabbed DW's hand holding the meat. At 09:03:34 h,

FW grinned, pant-screamed slightly, and then reached for the meat. FW eventually obtained a small amount of meat which DW had removed from his mouth. DW then climbed further up the tree and left FW, ending the interaction, at 09:03:51 h.

DISCUSSION

In the present case, a non-estrus female, FW, after several types of sociosexual behaviors, such as touching the penis, fellatio, and genito-genital contact without penile insertion, begged DW for bushpig meat by extending her hand to the mouth of DW. This is the first such report of fellatio between opposite-sex adult chimpanzees and is also the first report of fellatio in the context of food sharing.

Sociosexual behaviors during food sharing have been reported in wild chimpanzees and have been interpreted as actions performed to reduce social tension (Sandel & Reddy 2021). Thus, it can be assumed that the series of sociosexual behaviors in this report also served to reduce tension. Alternatively, such behavior may function as begging, because typical begging behaviors, such as peering into the face and reaching for the mouth, also occurred. Gilby (2006), who studied begging behaviors during meat sharing, classified them according to their intensity, from milder to more intense: (1) sitting close to the meat holder and peering at him, (2) reaching out to the meat holder (no contact), (3) touching the meat holder, and (4) reaching a hand near to the meat holder's mouth and mak-



Figure 1. Fellatio between FW (right) and DW (left)



Figure 2. FW (right) pressing her sexual skin to DW's (left) erect penis



ing contact with it. The series of sociosexual behaviors observed in this study, if they were considered begging behaviors, would be classified as category (3). However, several behavioral elements observed in this study were not reported in Gilby's behavioral repertoire of begging. In addition, according to Gilby's definition of harassment during meat-eating, the observed behaviors were not considered harassment, because there was no contact with DW's mouth or hands, nor was his behavior restricted. Although it is difficult to conclude from just one case, the series of displayed sociosexual behaviors may have occurred to reduce tension, so that FW could then make a smooth transition to begging behaviors.

The connection between meat sharing and sexual behavior in these observations may seem relevant to the meat-for-sex hypothesis (Stanford 1996), especially regarding reciprocation on a long-term basis (Gomes and Boesch 2009). In this case, however, it is unlikely that there was an immediate reciprocal exchange of meat sharing and mating opportunities for two reasons. The first is that the female was non-estrous and lactating, which means copulating with her would not lead to pregnancy. The second is the negative responses of DW, such as turning away after a series of sociosexual behaviors. In this case, even though meat sharing occurred after the begging behaviors, it appeared unlikely that DW gave meat in immediate return for the sociosexual behaviors of FW.

Fellatio is considered rare because males are at high risk of exposing their vital organs to other chimpanzees' mouths. It has been proposed that such high-risk behaviors can be used to test and strengthen alliances between same-sex partners (Kirkpatrick 2000). For chimpanzee males, forming alliances with other males is crucial. Thus, for a rare case of male–male fellatio, such a function of strengthening male–male relationships was emphasized (Brooker *et al.* 2020). However, as reported in this study, fellatio can occur between a female and a male in the probable context of tension reduction. Thus, the function that is used to test social bonds may also apply to opposite-sex partners.

This report describes a very rare case of heterosexual fellatio observed in the wild. However, it is difficult to know why such behaviors are rare and why this case occurred in this context. More such observations are needed to gain a deeper understanding of sociosexual behaviors as well as the function of fellatio in chimpanzees.

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MWCS under COVID-19 crisis

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Firstly, I would like to express my deepest gratitude to all our members for your continued support.

Founded in 1994, Mahale Wildlife Conservation Society (MWCS) has provided a forum for researchers on the two *Pan* species involved in fieldwork across Africa to share information on research and conservation through the publication of Pan Africa News. Another mission of ours is to contribute to wildlife conservation in the chimpanzee habitats of western Tanzania, particularly in the Mahale Mountains National Park.

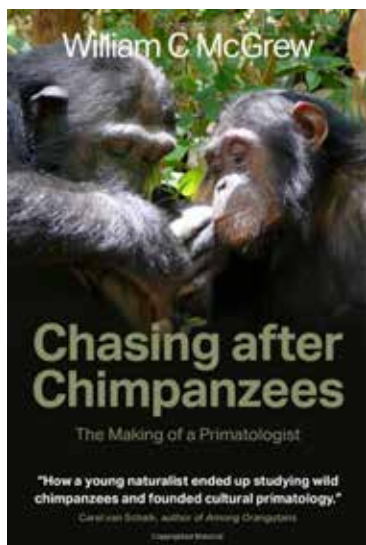
MWCS has been engaged in three projects in Mahale. Firstly, we have supported the park headquarters at Bilenge to improve their facilities, for example, by donating a visitor center and creating tourist exhibits to be displayed there. Secondly, we have promoted community-based conservation at villages such as Katumbi outside the park. The proactive involvement of local communities is vital for successful wildlife conservation. For this purpose, we have prioritized the improvement of social infrastructure, such as primary education and a dispensary in Katumbi, with the aid of the Embassy of Japan in Tanzania. We have produced *Wanyama wa Mahale*, an animal guide written for local children with a grant from the Toyota Foundation. Since 2009, MWCS has awarded special scholarships to three outstanding youths who aspire to pursue higher education to contribute to their community. The third project is to enhance environmental conservation in and around Mahale. For example, a project to control *Senna spectabilis*, an invasive alien plant species, was successfully implemented in collaboration with the National Park management. Importantly, as the

risk of zoonotic infection from humans to chimpanzees has heightened with the increase in the number of tourists, we have instructed tourism operators to take effective measures to prevent viral transmission, such as the wearing of masks during observation and maintaining an appropriate distance from the wild apes.

These activities would not have been feasible without the assistance of research assistants belonging to the indigenous Tongwe community. Additionally, our activities are beneficial to them in that they earn cash income by assisting us with their traditional knowledge of nature in Mahale.

Since late March 2020, the researchers' fieldwork has been suspended due to the strict precautions against the spread of COVID-19. Our research assistants have been maintaining minimal activities inside the park, such as the maintenance of research trails and health monitoring of M-group chimpanzees. To help them stay in the park and continue their activities, MWCS-J contributed 300,000 yen in December 2021. Although the short-term outlook for our own activities is unpredictable, we are planning to return to the field as soon as possible, while keeping a close eye on the domestic and international developments related to overseas travels. By August, we hope to resume educational and medical support in Katumbi, which has been halted for the past two years.

We would be grateful if you would consider supporting our activities under the prolonged pandemic. If you are interested in joining MWCS or donating money, please contact us at info@mahale.main.jp. We will then inform you of the remittance methods and other details.



William C. McGrew

Chasing after Chimpanzees: The Making of a Primatologist

Gloucestershire: Mereo Books, 298 pp.

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Having moved from zoology to psychology to anthropology on both sides of the Atlantic, Bill McGrew developed a fascination for chimpanzees which led to him spending four decades studying our nearest living relations in their African homelands. He held a series of academic posts in the USA and UK, culminating in a professorship at the University of Cambridge and ending in retirement to Scotland. As he puts it: “I was lucky enough to be paid by various academic institutions to do what I would have paid them to let me do”. This memoir consists of a series of stories and vignettes from a varied and colourful life, mainly involving animals, and naturally focusing on chimpanzees. All proceeds will go to organisations that rescue and care for chimpanzees.

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