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40 years of research at the Taï Chimpanzee Project

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Almost 40 years ago, in the summer of 1979, Christophe and Hedwige Boesch arrived in Taï National Park, Côte d'Ivoire, to start the first chimpanzee long-term field site observing wild chimpanzees living in a primary rain forest. Christophe and Hedwige had chosen to study the chimpanzees in Taï, motivated by rumours that these chimpanzees would use hammers to pound nuts—a tool use not known in chimpanzees—and to provide data for a meaningful comparison with the savannah-woodland dwelling chimpanzees of Gombe and Mahale (Boesch & Boesch 1994).

After setting camp in the area of the UNESCO Man and the Biosphere Programme (Figure 1), they started to follow the chimpanzees and tried to habituate them without the aid of provisioning. Quickly they realised that the black shadows, they met occasionally in the forest, would dodge them again and again. After endless and unsuccessful attempts to come close to the chimpanzees and observe their behaviour, they decided to change their tactic and announce their arrival to the chimpanzees by tongue-clacking, in the hope the chimpanzees would look at them before disappearing and as such getting accustomed to the presence of the observers. Although there was no immediate improvement, by 1982 Christophe and Hedwige were able to have some direct observations. It took them, however, another two years, before the first individuals had enough trust to accept their presence even when resting. The year of 1985 marks the beginning of data collection in the first community of Taï chimpanzees, the North group (Boesch & Boesch-Achermann 2000).

The first years of the Taï Chimpanzee Project, Christophe and Hedwige focused on the nut-cracking behaviour and the hunting behaviour. Very quickly they observed that the chimpanzees in Taï would use wooden and stone hammers, depending on the hardness of the nut shell, cracking at least five different types of nuts (Boesch & Boesch 1982, 1984). These observations were pioneering for the work on chimpanzee cultures that started at a later point in time (Whiten *et al.* 1999). At the same time Christophe realised that yet another behaviour, thought to

Figure 1. North Camp of the Taï Chimpanzee Project in 2018 in the middle of the National Park. This is the original camp Christophe and Hedwige Boesch were living with their family until the 1990s (photo courtesy of Tokyo Broadcasting Station).

be prominently involved in human evolution, was common in the Taï chimpanzees: cooperative hunting for monkeys (Boesch & Boesch 1989; Boesch 2002).

Starting in the late 1980s, Christophe and Hedwige were joined by field assistants from the villages close by to help them observing the behaviour of the chimpanzees. Gregoire Nohon and Honora Kphazi were the first ones to follow chimpanzees and became the role models for many young people from the villages, who came to the Taï Chimpanzee Project to work. With these two, the longterm data collection of behavioural focal observations started in the early 1990s.

When Christophe Boesch became director of the newly founded Max Planck Institute for Evolutionary Anthropology (MPI EVA) in 1997, the heydays of the Project started. Project staff habituated three additional neighbouring communities: South and Middle group were finally habituated in 1997 and 1998 respectively, and in East group staff started to collect behavioural data starting in 2007. Students from the MPI EVA came to Taï and investigated wide ranges of topics in behavioural ecology related to conflict (Wittig & Boesch 2003, 2010), communication (Crockford & Boesch 2003; Herbinger *et al.* 2009), cognition (Normand *et al.* 2009; Sirianni *et al.* 2015), competition (Anderson *et al.* 2002; Deschner *et al.* 2004; Stumpf & Boesch 2005), cooperation (Gomes & Boesch 2009, 2011), culture (Luncz *et al.* 2012), conservation (Campbell *et al.* 2008) and many other topics. At the same time the Taï Chimpanzee Project also hosted international researchers from outside the MPI, adding expertise to the project (*e.g.*, archaeological techniques (Mercader *et al.* 2002), anatomical expertise (Zihlman *et al.* 2004)).

The Taï Chimpanzee Project, however, also suffered setbacks. The chimpanzee population had to cope with extensive individual losses due to zoonotic diseases transmission from human respiratory viruses (Köndgen *et al.* 2008). Only after rigorous quarantine and hygiene rules with strict reinforcement in the years 2010–2012, respiratory disease transmission was stopped (Grützmacher *et al.* 2017) and the population started slowly to recover. A veterinary program led by Fabian Leendertz of the Robert Koch Institute in Berlin (Germany) guarantees the constant presence of a qualified veterinarian in the field. This program, apart from its crucial contribution to the chimpanzee health, has also discovered a wide range of pathogens with formerly unknown effects on chimpanzee (*e.g.*, Hoffmann *et al.* 2017).

Planning for his retirement, Christophe Boesch handed over responsibility for the Taï Chimpanzee Project to Roman Wittig and Catherine Crockford in 2013. Since then staff members habituated a sympatric living sooty mangabey group, in order to compare the socio-ecology and cognition of both species (Mielke *et al.* 2017, 2018), and started to habituate the fifth community of chimpanzees in the Northeast of the research area, allowing us to better observe intergroup encounters (Samuni *et al.* 2017). With Cathy and Roman leading the project, research took new direction using supporting hormonal measures (Samuni *et al.* 2018; Preis *et al.* 2018), experimental work (Crockford *et al.* 2017; Sirianni *et al.* 2018) and additional comparative set-ups with other species (Surbeck *et al.* 2017a,b).

The Taï Chimpanzee Project will celebrate 40 years of research with an international scientific symposium held 29–31 May 2019 at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. During the year 2019 a book looking back at 40 years of research in Taï will be published by Cambridge University Press.

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Use of Wild Date Palm (*Phoenix reclinata*) by Mahale Chimpanzees: A Likely Case of Social Learning via Direct Observation

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INTRODUCTION

The propagation of knowledge from one individual to other group members is an essential aspect of chimpanzee (*Pan troglodytes*) culture (McGrew 2004). It is important to record when and how chimpanzees acquire new knowledge. Furthermore, it is useful to know how novices learn the innovation and to what extent they can replicate the behavior, so as to provide insight into whether the information will propagate through the group. The M-group chimpanzees in Mahale Mountains National Park, Tanzania, customarily fish for ants. They do so by creating probes from many kinds of plant materials, inserting these into the entrance of the nest of wood-boring carpenter ants (*Camponotus* spp.), then withdrawing the probes, and eating the ants (Nishida 1973; Nishie 2011). Chimpanzees in some regions utilize the wild date palm (*Phoenix reclinata*, hereafter date palm) for different purposes. For example, chimpanzees in Toro-Semliki, Uganda, eat the fruits of date palms (McLennan 2013) and squeeze the stem of the date palm into their mouths (McGrew & Hunt 2011). Although date palms are also common in the M-group's home range (Itoh 2015), there have been no previous reports that the M-group chimpanzees have utilized date palms for ant-fishing. In this article, I describe the first documented observation in Mahale of two chimpanzees processing date palm to use as probes for ant-fishing.

METHODS

I have intermittently studied habituated wild chimpanzees (*P. troglodytes schweinfurthii*) of the M-group since January 2002 (see Nakamura *et al.* 2015 for details of the research site). The research period of this study was from August 24 to 31, 2018. All the group members have been identified and named, and the demographic data, such as kinship, estimated date of birth, and immigration into the M-group, is available to researchers. Focal animal sampling was used to collect data with a continuous recording method (Martin & Bateson 2007). Data was recorded with a digital video camera (Sony HDR-CX430V) and on field notes. KP, KP18, JR, and XT in the description refer to the names of individuals. The sizes of the used objects were estimated, since they could not be collected.

OBSERVATION

At 12:53 h on August 30, 2018, I started to follow KP18 (4-month-old male) along with his mother, KP (approximately 15-year-old female). At 14:10 h, KP was holding her infant son KP18 clasped to her belly and started to eat the pith of a woody vine, *Landolphia owariensis*. Carpenter ants inhabiting the tree and entrance holes of the ants' nests were visible 3 m above the tree trunk. Date palms were growing next to the tree, and the leaflets covered the trunk. At 14:11:30 h, KP climbed up the vines, approached the hole of an ant nest, and tore up a leaflet of a date palm from the tip to the rachis to make a probe (length: ca. 60 cm; width: ca. 0.5 cm). Then, she started to fish for ants using the probe with her right hand, and had a spare probe held in her left groin pocket. At 14:15:12 h, KP bit off the tip of the probe to adjust it and continued ant-fishing.

At 14:17:03 h, JR (5-year-old female) approached KP whilst pant-grunting. At 14:18:11 h, JR approached KP and started watching her fish for ants at close range (Figure 1). At 14:18:41 h, JR sitting on a vine bit the tip of a leaflet of a date palm, tore it up with her mouth and hands, and removed it at the rachis. JR adjusted the tip of the leaflet by biting it (length: ca. 70 cm; width: ca. 0.7 cm) and again watched KP fishing for ants. At 14:19:13 h, JR started to fish for ants next to KP.

At 14:20:00 h, KP climbed down the tree, leaving the probe in the hole and walked away with KP18, while JR continued ant-fishing. At 14:20:06 h, JR moved to the hole, which KP had used moments before, and continued fishing. At 14:20:13 h, JR climbed down the tree and walked away. At 14:20:17 h, XT (approximately 26-year-old female) climbed up and removed a part of the vine of *L. owariensis* (length 20 cm, and width 0.5 cm, approximately) to start fishing for ants at 14:20:31 h, in the hole that KP and JR had both used. See Video 1 available online at http://mahale.main.jp/PAN/2018/010.html.

After the 8-days of this study, I checked the long-term records, and also asked researchers and research assistants whether they had observed the M-group chimpanzees using date palm for ant-fishing. None of them had ever observed the usage of wild date palm for ant-fishing by the M-group members.

DISCUSSION

Two non-kin females used the leaflets of a date palm to fish for carpenter ants. For more than fifty years of study in the M-group and the extinct K-group (Nishida

Figure 1. KP is removing ants from the probe made of date palm (left). JR (right) is watching KP's actions. The leaflets of the wild date palm are covering the tree from the right side. This figure was captured from the video.

& Hasegawa 1982), researchers have never observed the Mahale chimpanzees using date palm for ant-fishing until this instance. Of course, this does not necessarily mean that they have never actually used date palm. In the home range of the M-group, three Palmae species occur: date palm, palmyra palm (*Borassus* sp.), and oil palm (*Elaeis guineensis*) (Itoh 2015; Itoh & Nakamura 2015). Albeit rare, there are a few reports that Mahale chimpanzees ate piths of the oil palm (Zamma *et al.* 2011). Thus, the possibility cannot be excluded that the Mahale chimpanzees, including KP and JR, already had experience handling Palmae species infrequently and acquired knowledge of the physical features of the leaflet of date palm before this instance. Even so, it is certain that they have used date palm only at low frequency, since no researchers so far had noticed. Nishida *et al.* (2009) operationally defined an innovation as a behavioral pattern seen by observers for the first time after a sufficient time of long-term observation passed. Here, recognizing these observational limits, KP's use of date palm may be regarded as an example of innovation, according to this operational definition.

Each action constituting ant-fishing using date palm by both individuals, KP and JR, seems similar to those using common materials for ant-fishing. Their ant-fishing processes involved all four actions that typically constitute ant-fishing behavior; creating probe, inserting probe, withdrawing probe, and removing ants from probe (Nishida 1973; Nishie 2011). In addition, it took KP and JR only a few seconds, at most, to create the probes from date palm and they also prepared spare probes. Since they could create probes with the purpose of fishing for ants from possibly unfamiliar materials through acquired techniques, KP's case is not considered as an innovation of a novel behavior itself, but as an upgrade of knowledge on available materials to create tools (Nishida *et al.* 2009).

A juvenile female, JR, closely watched KP fishing for ants and then started processing a leaflet of date palm and fished for ants with the tool she made, next to KP, despite having never or rarely used date palm before, nor observing the tool making process by KP. It is unlikely that two chimpanzees independently started using the unfamiliar material in close succession. JR's acquisition of the knowledge to use the date palm suggests that social learning via direct observation played an important role in transmitting the knowledge from a skilled individual to a novice (Nishida *et al.* 2009). JR created an ant-fishing tool from a leaflet of date palm without watching the model's (KP's) actions, and JR already knew the techniques of how to create ant-fishing probes with plants that the M-group members normally used. Thus, the social learning in JR's case is likely to be emulation (Boesch & Tomasello 1998). That is, JR may have observed KP's ant-fishing and inferred that the material of her probe was made from a leaflet of the date palm that was growing near the tree where the ant-fishing was occurring. After inferring the goal of making a probe with new material and comprehending the physical features of the leaflets of date palm, which have parallel veins (Tomlinson *et al.* 2011) making it easy for chimpanzees to tear the leaflets from the tips to the rachis, JR created a probe by trial-and-error. This observation supports previous reports, such as the mechanism of propagation of a tool using technique from one innovator to a novice through social learning via direct observation in the Sonso community of the Budongo Forest, Uganda (Hobaiter *et al.* 2014).

It is important to keep accumulating data on newly acquired knowledge and the propagation process among group members in order to understand what produces cultural differences among wild chimpanzee groups.

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A Short-Term Visit of an Adult Male Bonobo from the Neighboring Unit-group at Wamba

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INTRODUCTION

The social organization of male-philopatry is often explained by the importance of cooperation among kin-related males to defend their group territories and the encompassed females against other neighboring groups (Williams *et al.* 2004; Furuichi 2006). Strong hostility between males of different groups may make male visit and immigration into neighboring groups extremely difficult. In chimpanzees (*Pan troglodytes*), there is a higher likelihood of intergroup killing when large male parties encounter smaller male parties or lone males of different groups (Wrangham 1999). In reality, visiting males (temporary immigrants, see Nishida *et al.* 1999) have been only observed twice in Bossou, Guinea (Sugiyama 1999) during the period of over 55 years observing wild chimpanzees at multiple study sites. It has been observed that male bonobos (*Pan paniscus*) have more tolerant relationships with out-group males than do male chimpanzees (Sakamaki *et al.* 2018). Therefore, the obstacles to visit or immigrate faced by bonobos might be less than those encountered by male chimpanzees. However, there has been only one report of male visits at Lomako (Hohmann 2001) and one report of male immigrations at Wamba, Democratic Republic of the Congo (Hashimoto *et al.* 2008). Here, we report an additional case of a temporary visit by an adult male bonobo from a neighboring group at Wamba. Moreover, the social condition and motivation of his visit are discussed referring to other cases of the *Pan* species in this report.

BACKGROUND

The observations in this report were collected from a group of wild bonobos, called PE, at Wamba, Luo Scientific Reserve, the Democratic Republic of the Congo, where long-term observations have been conducted since 1974 (Hashimoto *et al.* 2008). Since 1976, a bonobo group, called P, was being studied occasionally until the interruption of all research in 1996 due to the civil war (Tokuyama & Furuichi 2016). In September 2010, habituation and identification of bonobos in the antecedent P group's range were initiated. Researchers realized the existence of two independent groups ranging the area, and named these two groups PE and PW, respectively. The research was focused on the PE group with observations made on a daily basis (Sakamaki *et al.* 2018). It was suggested that the PE group is probably identical to the P group since two parous females from the P group were present in the PE group (Tokuyama & Furuichi 2016). At the time of this report, the PE and PW groups consisted of 28 (including 9 adult females, 5 adult males, no adolescents) and 16

Figure 1. Terry was estimated to have been born in 2000 (17 years old at the time of this observation).

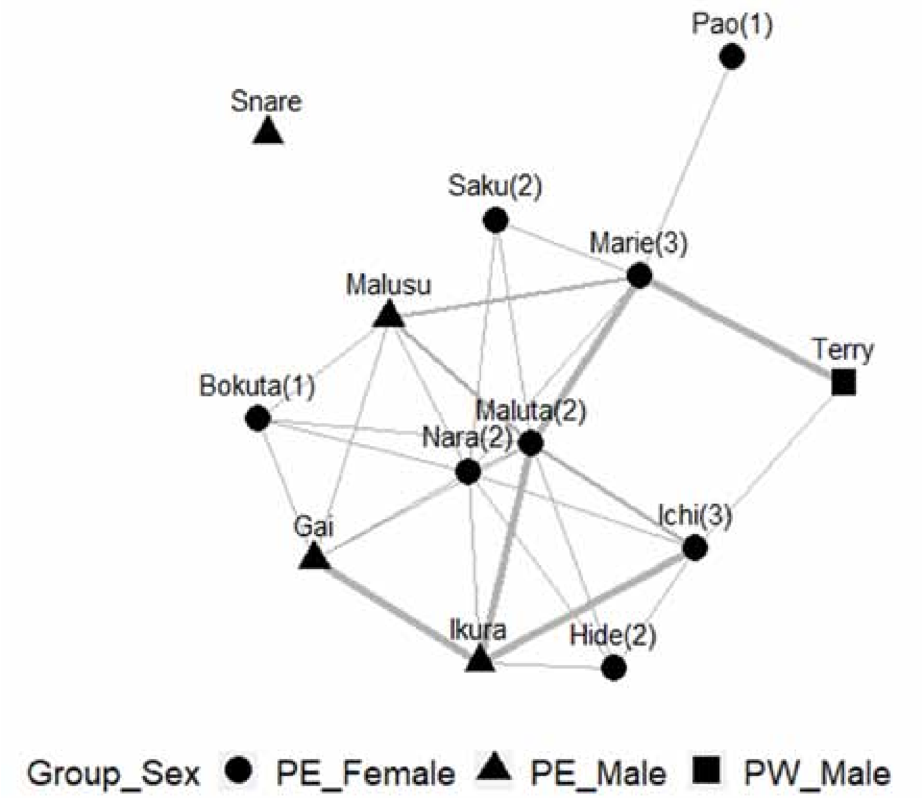

Figure 2. Proximity network among individuals. The node shows an individual and its shape is classified by the group and sex of the individual. The edge shows a proximity between individuals and its thickness is related to the frequency of the proximity. The line thickness shows a number of the proximity between individuals at scans. The number in parenthesis means a score of the sexual skin in each female, (1) non-swelling, (2) intermediate swelling, and (3) maximal swelling.

individuals (including 7 adult females, no adolescent females, 3 adult males, 2 adolescent males), respectively. It was observed that the PE group frequently encounters the PW group (396 days in 1478 observational days between 2012 and 2015; Sakamaki *et al.* 2018). Additionally, one or two adult females of the PW group occasionally stay for a few days in the PE group after the other PW individuals apparently separated from the former (Tokuyama unpublished data). However, PW males had never been observed to remain in the PE group after the two groups separated. The visitor male of this report, named Terry, was identified in the PW group as an adolescent male on October 2012 (Figure 1). Although there was not sufficient data regarding the aggressive dyadic interactions required to assess the dominance hierarchy among the males of the PW group, Terry was apparently middle to low ranking in the group. KT, one of the authors, recorded all the perceived social interactions, as well as all individuals within visual range and within 5m proximity at every 15 min scan on June 29, 2018.

OBSERVATIONS

On June 28, 2018, local assistants found Terry together with the individuals of the PE group at 16:59 h just before the night beds were made, although no other bonobos of the PW group had been observed since 14:44 h on June 26. On that day, the party of the PE group included all the individuals except for the alpha male, named Turkey, and his mother, named Kabo.

The next day, we arrived at the site at 06:07 h and found Terry getting out of his night bed at 06:46 h (Figure 1). His bed was made higher than others and was about 30 m away from the nearest bed of another adult female of the PE group. At 07:03 h, Terry exposed his erect penis and solicited an adult female, named Ichi, with maximal swelling. He was approached by Ichi, and they copulated with each other.

Terry was positioned at the periphery of the group during rest and travel. At 08:20 h, when the bonobos were feeding on the fruit of the *Landolphia* sp., a higher-ranking female, named Hide, chased Terry out. After he fled with a scream, the observers lost sight of Terry from where the other individuals were eating or resting.

At 11:43 h, Terry appeared again at a distance of about 50 m from where the PE bonobos were feeding on the *Landolphia* fruit at another location. At 11:52 h, Terry approached and sat within 5m of an adult female with maximal swelling, called Marie. At 11:54, Terry solicited Marie with an erect penis and copulated with her. At 11:55 h, Terry exchanged grooming with Marie for 43 min.

At 12:38 h, when Marie and the other individuals climbed down from the trees and began to rest together on the ground, Terry was not in the vicinity. After this, Terry was not observed until August 8, 2018, when the party of the PE group encountered individuals of the PW group. In all, Terry had been observed in the proximity of only two adult females with maximal swelling (Figure 2).

DISCUSSION

Terry had approached two females with maximal swelling but kept a distance from the other PE individuals on the day we observed him. He seemed afraid of PE individuals, although aggression was not directed towards him by any PE males. The absence of an alpha male in the PE group may have facilitated Terry's visit, because higher-ranking males tend to behave more aggressively toward out-group males during intergroup encounters (Tokuyama *et al.* unpublished data). When the PE and PW groups frequently associate with each other, Terry was occasionally observed to have engaged in affiliative interactions with PE individuals (Tokuyama, unpublished data). Such affiliative interactions through intergroup encounters might be one of the reasons for the tolerance from the PE males towards Terry during his visit. There is a possibility that the PE and PW groups had divided from one group before 2010 when the intensive study of the PE group was initiated. Accordingly, Terry might have spent his childhood with the PE males. However, genetic analysis indicated that he had not been fathered and mothered by any PE individual, although one PW male remained his potential father (Ishizuka, unpublished data).

In this report, the sex ratio (the number of females to males) was a little higher in the PE group (1.8) than the PW group (1.4). Additionally, between June 23–24 (4–5 days before the observation of this report), there was only one female with maximal swelling among the seven females of the PW group. Terry copulated with two females of the PE group outside his own PW group. At Lomako, in a bonobo group called Eyengo, when the number of adult females to males had doubled compared to the previous years, two strange males visited for 12 months. One of the males had developed friendships with some Eyengo residents while receiving aggressions and copulated with one of the females three times (Hohmann 2001). These cases suggest that male bonobos might visit neighboring groups to seek additional mating opportunities.

In another case of bonobos at Wamba, four or five adult males and two females with infants had settled a study group, called E1, when some individuals of the E1 group disappeared and two neighboring groups ceased to exist probably due to poaching during the civil war (Hashimoto et al. 2008). However, in two chimpanzee groups at Mahale, Tanzania, called K and M groups, when K males had disappeared one by one, only K females visited or immigrated into the neighboring M group with their dependent offspring (Nishida *et al.* 1985). These cases indicate that male bonobos might be more tolerant of strange males than are male chimpanzees.

At Bossou, two strange males had visited a study group living in an isolated forest, but they did not suffer particular aggression from resident males. In Bossou chimpanzees, intragroup male cooperation might be less intense than that in other chimpanzee groups. This is because they do not have competitive adjacent groups, while they compete within their own group for restricted resources in their fragmented ranging area (Sugiyama 1999). If the intragroup competition is greater than intergroup competition, male immigration might occasionally be a beneficial strategy.

In conclusion, Terry's temporary visit to a familiar neighboring group might have been a tactic to gain mating opportunities, which is possible among Wamba bonobos tolerant of neighbors.

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Leopards Attempted to Hunt Wild Chimpanzees at Mahale

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INTRODUCTION

The relationship between chimpanzee and leopard (*Panthera pardus*) is threefold: chimpanzee intimidates, attacks, and/or kills leopard (Gandini & Baldwin 1978; Hiraiwa-Hasegawa *et al.* 1986; Boesch 1991); leopard attacks and/or preys upon chimpanzee (Boesch 1991, 2009; Nakazawa *et al.* 2013); and chimpanzee scavenges the prey hunted by leopard (Nakamura *et al.* in prep.; Hasegawa *et al.* 1983; Nishida 1994, 2012). Understanding the relationship between chimpanzee and leopard (or other potential predators) has been considered important in order to reconstruct human evolution. Social structure may be affected by predator–prey relationships, feeding strategies, and cooperation against predators, but direct observation of encounters between chimpanzee and leopard have been few, since leopard is rarely habituated to human observers and thus tends to be elusive (Gandini & Baldwin 1978; Boesch 1991, 2009; Pierce 2009; Nakazawa *et al.* 2013). Here I report a case in which two leopards attempted to hunt an adult female chimpanzee and her two offspring at Mahale, Tanzania.

METHODS

I did my field research on the M group chimpanzees at Mahale in August 2018 (See Nakamura *et al.* 2015 for the details of the M group chimpanzees and the research site at Mahale). The chimpanzees who barely escaped from being hunted by leopards were an adult female, Omo (estimated 22 years old), and her two sons, Omali (7 years old) and a 17-months-old infant (yet unnamed, hereafter OM17). Most members of the M group ranged and stayed high up in the mountain area to the east of the M group's home range, and a few chimpanzees were observed in the lower, flatter area through this month.

OBSERVATION: 25 AUGUST 2018

The main party of M group chimpanzees still seemed to be ranging in the mountainous area on this day, since we had heard no calls nor found any signs of chimpanzees, as I and a research assistant, Bakari Rashidi, had been searching for chimpanzees in the flatter area of the M group's home range since morning.

At 9:50 h, we heard a "faw!" bark about 50–100 m away from where we walked. We supposed it to be a chimpanzee bark, but while we walked along the research trail with noisy footsteps in dry leaves, the bark was too sharp and short to pinpoint its source.

Then, we separated, seeking to find the chimpanzee who had emitted the bark. After a while, I heard another "faw!" bark from the direction in which the assistant had headed, and then I followed it into the bush, while hearing the barks again and again.

At 10:02 h, I found Omo, with OM17 ventral, and Omali on a bough of a tree about 3 m above the ground. At the same time, the assistant came out from the bushy undergrowth and told me that, when he had arrived there, he had seen a leopard on the ground under the tree in which Omo family stayed. The leopard had looked up the Omo family sitting on the bough and thus seemed to attempt to hunt them in the tree, but Omo had managed to repel it by persistently emitting barks. He also saw the leopard run into the bush on my arrival, although I did not notice that. After that, Omo sitting on the bough ceased to emit barks, and kept staring carefully into the bushes where the leopard had concealed itself.

At 10:03 h, a growl of a leopard like "grururu..." was heard from the bush about 10 m away from us where we stood by the tree. Omo, still with OM17 ventral, and Omali on the bough silently stared toward the bush. At 10:06 h, another growl came from the same place in the bushes. Omo and Omali kept silent on the bough staring in that direction.

At 10:09 h, the Omo family silently started to move southward through the trees.

At 10:10 h, another roar of a leopard like "gwa-gwa-gwa" was heard from the bush about 10 m away from the first growl, while the first growl still continued, so we realized that there were two leopards present! At 10:13 h, the leopards remained growling there. At 10:14 h, as the Omo family went out of our sight, we stopped observing and retreated to a research trail nearby.

At 10:21 h, we arrived at a research trail and still heard the leopards' growls from the bush. Then, we left there to search for other parties of chimpanzees; however, we did not find any other chimpanzees nor hear any calls of chimpanzees, until we saw the Omo family again at 14:18 h. They were then about 500 m north of the tree where the leopards had attempted to hunt them. We were relieved to see them again without any wounds.

DISCUSSION

This report presents the first direct observation of leopards' attempted hunting wild chimpanzees from East Africa, although some cases have been reported from West Africa (Boesch 1991, 2009). Although previous reports from eastern and central Africa have provided fecal evidence and some indirect observation of leopard predation on wild chimpanzees (Furuichi 2000; Nakazawa *et al.* 2013), it has been difficult to observe such cases directly, perhaps because leopards have not been habituated to humans. In this case, however, two leopards stayed close to human observers; further, they growled and roared at us, although they hid themselves in thick undergrowth upon my arrival. This twofold reaction of the leopards to human observers, threatening and concealing themselves, may reflect the recent progress of leopard habituation to humans in Mahale (Nobuko Nakazawa, unpublished data). As a result, they now can confront or even threaten humans on encounter, though they still seem somewhat afraid of humans, concealing themselves in the bush. Thus, our arrival at the place where leopards were attempting to hunt chimpanzees might deter leopards from persisting in attempting to hunt chimpanzees (Boesch 1991, 2009). Accordingly, we might have saved the lives of the Omo family.

Previous studies have discussed to what extent leopard predation pressure on chimpanzee affects their social structure (Boesch 1991, 2009). Our observation indicates that chimpanzees are vulnerable to leopard predation, at least when they are in small parties or when they have dependent offspring. Since chimpanzees have flexible fission-fusion association, they often disperse in small parties or even alone. When chimpanzees range alone or only with their dependent offspring, predation risk by leopards may increase. In particular, infants and juveniles may risk being hunted easily by leopards, unless they obtain enough support from adult apes, such as their mothers and adult males. On the other hand, when they are in a large party including adult males, they outnumber a leopard, thus they deter it from attempting to hunt them or even chase away it, as suggested in some previous studies (Nakamura *et al.* in prep.; Boesch 1991, 2009; Pierce 2009). This incident indicates that leopard predation pressure on chimpanzees may affect their association patterns, possibly making Mahale chimpanzees, especially females with dependent offspring, more gregarious than those in other populations without sympatric leopards or other predators.

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Why Don't Chimpanzees Use Stones as Lethal Weapons? A Murder Mystery

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On 11 November, 2018, BBC showed a one-hour-long documentary on the wild chimpanzees of Fongoli, in Senegal. These are the first savanna chimpanzees to be fully habituated, by the persistent and patient efforts of Jill Pruetz and her team. The film is part of David Attenborough's five-part 'Dynasties' series, and, like his previous efforts ('Life on Earth', 'Blue Planet', etc.), it is likely to be shown worldwide.

Its contents prompted me to pose the titular question, which puzzles me, so that I seek clarification or correction from the readers of *PAN*. To explain, the film's storyline follows the trials and tribulations of the alpha male, David, as he is savagely gang-attacked, and left for dead, with horrendous injuries. This extreme form of male-male competition is not new, as it has been recorded elsewhere in Africa, for example, at Gombe with Goblin, and at Mahale with Kasonta (Nishida 2012, pp. 235–236).

As the narrative unfolds, we see many superbly filmed episodes of displaying male chimpanzees, with all the elements that seem to be chimpanzee universals. Among these are many incidents of stone-throwing, most apparently as un-aimed flings than as aimed ballistic weapons targeted at opponents. Several camera shots show us that suitable stones are super-abundant, especially on the open and wide laterite plateaux. Pieces of laterite ranging in size from oranges to basketballs, lie about on the surface, readily picked up. (Laterite is a porous, friable stone, which often fractures on impact, especially after extensive weathering. It would not be useful for nut-cracking but makes easily thrown missiles.)

The climactic attack involves at least four adult males piling on to David, using hands and teeth. In the process, David loses at least one digit, and has severe slashing wounds to the scrotum and thigh. (We do not see wounds, if any, inflicted by him on his attackers.)

Which brings me to the title of this comment: Why doesn't one or more of the attackers just pick up a stone and hit David on the head? A single blow from the powerful upper limb(s) of a chimpanzee with a hand-held hammer-like weapon would render him unconscious or dead.

Not only does this weapon-use NOT occur in this particular case, but so far as I know, such a simple solution to the problem of dispatching an adult male fighting for his life has not been reported in previous gang assaults, at any field site. (Or even in less dramatic confrontations, even between one-on-one fights.)That is, stone tool use in agonistic display is common, especially in the lead-up to physical assaults, as shown here, but the actual attack entails use of the hands, feet and teeth only.

So, how to explain this conspicuous absence of hand-held percussive weapon-use? Stones used as missiles is well-known, dating back to Goodall's (1964) seminal paper published decades ago, which drew the first distinction between aimed and un-aimed throwing at Gombe. That chimpanzees make creative use of such thrown stones is exemplified by Mahale males heaving stones into streams to produce impressively noisy splashes that augment the effects (Nishida 2012, p. 219).

One might hypothesise that only chimpanzees who know of the effects of lithic percussion in other spheres would think to generalise this to weapon-use. However, the well-studied nut-cracking populations, also from West Africa, at Bossou and Taï *do* use percussive technology in food processing, but not as hand-to-hand weapons, so far as I know. The Fongoli chimpanzees do not use hammer-and-anvil in extractive foraging, but *do* smash baobab fruits on stone anvils by hand.

It may be that suitable stones are scarce raw materials elsewhere, compared with their abundance at Fongoli. (And at Mt. Assirik, McGrew *et al.* 1981). This absence of suitable raw materials might apply to evergreen rain forest populations of chimpanzees, especially in equatorial Africa. But well-studied mosaic sites such as Gombe and Mahale have plenty of stones, as evidenced by their use in display. To test this idea properly across sites would require detailed geological data, not just of the presence and distribution of the right-sized and shaped stones, but also of their extent of embeddedness in the substrate. It might be that gang attacks occur in places where stones are absent, by intention. To my knowledge, such systematic data have not been gathered.

Perhaps wild chimpanzees are not aware of the potentially damaging effects of hand-held percussive weapons? But this is belied by their use of sticks and boughs as clubs in display. Such beating of conspecifics with wooden tools has been described in other populations, for example males striking females at Kanyawara (Wrangham, unpublished data). So why not extend this utility to stones?

Chimpanzees engaged in agonism may exercise self-restraint, just as in many other animal species that do not extend male-male contest competition into fatal realms. Perhaps they are content to inflict injury but not inclined to direct killing? That is, as was the case with David, the attackers 'left him for dead', but amazingly he survived. This hypothesis may be untestable, and would require evolutionary modelling, but it seems unlikely to me.

Chimpanzees show lethal aggression in killing members of neighbouring groups, some of which they have known well, that is, not strangers, but no lethal hand-held weapons have been involved. Attackers in any case also risk being injured themselves, so efficient and conclusive ways of defeating the opponent would seem to be favoured by selection, all other things being equal.

It is always tricky to seek to explain the absence of a behavioural pattern (e.g., McGrew *et al.* 1997), but sometimes a conspicuous absence compels attention. Further thoughts or data on this mystery would be useful.

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Four Cases of Grooming Sessions between Chimpanzees and Guenons at the Kalinzu Forest Reserve, Uganda

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Owing to a technical error, a number indicating affiliation and address of some authors was typed incorrectly as "2 *Primate Research Institute, Kyoto University, Aichi, Japan*" instead of "3 *Primate Research Institute, Kyoto University, Aichi, Japan*" in the print and the KURENAI versions. This error has been corrected in the HTML version at http://mahale.main.jp/PAN/2018/003.html.

Prof. Akisato Nishimura (Formerly Known as Akisato Toyoshima): A Pioneer of Chimpanzee Research in Tanzania

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Prof. Akisato Nishimura (his former family name was Toyoshima), one of the pioneer researchers of chimpanzees in Tanzania, passed away on 23rd December, 2018 at the age of 80. Hereafter I will refer to him as "Kentatsu-san", as he was affectionately called by his friends, colleagues, and students (because the kanji characters of his first name "Akisato" can also be read as "Kentatsu").

Readers of *PAN* may well be aware that Kinji Imanishi and Jun'ichiro Itani started the Kyoto University African Primatological Expedition (KUAPE) in Tanzania (at the time, Tanganyika) in 1961 in order to habituate and study wild chimpanzees. They set up a research camp in Cape Kabogo on the shore of the Lake Tanganyika. At that time, Kentatsu-san was a graduate student in Imanishi and Itani's lab. and thus was sent to the Kabogo Camp in 1962. He worked on Kabogo chimpanzees together with his senior classmate, Shigeru Azuma, until 1963.

The habituation of Kabogo chimpanzees was not successful due to the very steep terrain, but their study efforts have left precious early records of the ecology and social structure of wild chimpanzees that were least known at that time (Azuma & Toyoshima 1961–1962; 1965; Nishimura & Azuma 1977). Their pioneering spirit to elucidate chimpanzee social structure was inherited by various researchers and students, which finally led to the KUAPE team's success in habituating chimpanzees in the Mahale Mountains in 1965. Later, he left a note regarding the early days of KUAPE research (Nishimura 2012). This is a very important record about the historical background of chimpanzee studies in Tanzania.

Kentatsu-san later shifted his target species to woolly monkeys, muriquis, and spider monkeys in Colombia and Brazil (e.g., Nishimura 2003). Regarding his academic career, he served as an assistant professor at the Primate Research Institute of Kyoto University (1970 to 1977) and later became an associate professor of Doshisha University in 1977. He was promoted to the full professor of Doshisha University in 1989 and supervised students until his retirement in 2004.

Because he lived in Kyoto, he often visited the Laboratory of Human Evolution Studies at Kyoto University where many students, including myself, worked on Mahale chimpanzees. Every year in the spring time, we have our laboratory's annual mountain vegetable (sansai tori) event. After collecting many species of edible plants, we cooked them in the moutain cabin that Kentatsu-san owned in Kurama, a rural town in the mountains north of Kyoto City, and enjoyed them as tempura with cold beer cooled in the stream by his cabin.

Kentatsu-san will be greatly missed by everybody who knew him and worked with him.

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