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Chimpanzees digging up termites: A problematic but persisting issue

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Every chimpanzee researcher knows of the value of our study species in modelling the evolutionary origins of humanity. As our nearest living relations, with a Last Common Ancestor about 7–8 mya, *Pan* is the sensible starting point for etho-archaeology, that is, linking their behavior and artefacts to hominins who provide the latter but not the former. The aim of this essay is to show that such modelling should be done with care, lest we go astray, even in the simplest ways. A case study exemplifies this cautionary note.

This year marks the 20th anniversary of published findings inferring that *Australopithecus (Paranthropus) robustus* in South Africa used bone tools to dig into termite mounds in extractive foraging (Backwell & d'Errico 2001, d'Errico *et al.* 2001). Citing Goodall (Figure 1), the authors' conclusion was based on analyses of the use-wear patterns on the bones, that is, striations revealed by microscopy to have come from repeated abrasion with termite earth. They used experimental replicates of the artefacts to test their origin, by digging into extant termite mounds. Their conclusion was straight-forward: "*Our results suggest that early hominids used a bone technology as a part of their dietary adaptations, and they maintained a bone tool termite-foraging cultural tradition in southern Africa for nearly a million years.*" (Backwell & d'Errico 2001, p. 1362).

So, how has this assertion fared over the last two decades? Eight years later, the authors modified their claims, based on further analysis, but still stuck to the termite extraction hypothesis: "*Swartkrans and Drimolen tools may have been used to forage for termites, which remains the closest match, but also extract tubers, process fruits and conduct other, as yet unidentified tasks.*" (d'Errico & Backwell 2009, p. 1772). Others also continue to restate the argument: Lesnik (2011) has done the most extensive and sophisticated experimental study of bone tools and termite foraging, comparing *Macrotermes* and *Trinervitermes* (see below). She concludes that the evidence for termite foraging is stronger than tuber-digging in the Swartkrans bone tools. Also, "*South African weathered bone splinters used in unmodified form or occasionally shaped through grinding and implemented in foraging activities such as termite extraction.*" (Pante *et al.* 2020, p. 2).

These and other archaeological papers cite studies of chimpanzees using tools to get termites, so how apt is this linkage?

Chimpanzees consuming termites via tool use has been known for over 50 years, since Goodall (1964) first described termite fishing. Since then scores of papers have shown it to be the prevalent form of ape extractive technology, found from Tanzania to Senegal. New studies continue to report it in more populations and with more behavioral diversity (Boesch *et al.* 2020). So, what is the problem with Backwell *et al.*'s analogy?

Figure 1. Gombe chimpanzees' termite 'fish-in'. (Photo taken by Robert O'Malley)

First, wild chimpanzees have yet to be reported to use bone tools. Nor have captive chimpanzees, though some experiments have been done with other species in captivity, with mixed success.

Second, chimpanzees have not been seen to dig up termite mounds, with or without tools. They are well-known to do more than simple fishing with flexible probes: Some use tool sets of a

stout perforating/puncturing tool to access underground termite chambers, followed by prey extraction with a standard fishing probe (Sanz *et al.* 2004). But why is this activity not digging? If digging is defined as *excavation*, that is, displacing soil from the substrate, thus creating a cavity, then *compressing* soil by thrusting a stick into the ground is different (Estienne *et al.* 2017, Table 1, *cf.* McLennan *et al.* 2020, Table A).

Third, Backwell and d'Errico chose *Trinervitermes trinervoides* for their experimental digging into termite mounds (d'Errico *et al.* 2001). I can find no confirmed record of this genus being eaten by chimpanzees, either with or without tools, or from observations or fecal analysis. The genus appears to be absent from at least nine sites of chimpanzee research (Bogart & Pruetz 2008, Table II). *Trinervitermes* is in a different sub-family (Nasutitermitinae) of Termitidae than is *Macrotermes* (Macrotermitinae), which is overwhelmingly the preferred choice of chimpanzees across Africa (e.g. Collins & McGrew 1985, Lesnik 2011). *Trinervitermes* is small-bodied and squirts noxious chemicals from its snout; *Macrotermes* has the largest body-size of all termite genera and tastes palatable (Figures 2 and 3).

Fourth, carbon isotope data show that *Paranthropus* in South African had a diet of about 35% C_4 foods (Sponheimer *et al.* 2005), while chimpanzees almost exclusively consume C_3 foods, in both East and West Africa (Schoeninger *et al.* 1999, Sponheimer *et al.* 2006). Termite taxa vary greatly from pure C_3 to C_4 consumers, with the highest C_4 values coming from harvester (grass-eating) termites, such as *Trinervitermes* (Sponheimer *et al.* 2005). Thus, on multiple grounds, *Trinervitermes* seems to have been an unfortunate choice for modelling.

But how to explain the striated use-wear on the South African bone tools from antiquity, especially as the authors' original experimental replications indicate that it comes from digging termite earth? At least two alternative explanations are possible: (1) that the striations come from digging in a different but similar substrate, that is, a particular one in which soil particles are uniform in size and structure, as in the composition of termite mounds. (It seems likely that the size of such particles in mounds reflects the width of the gape of the mandibles of worker termites of any given species, but this idea seems not to have been tested.) Perhaps from digging up other dietary items in very sandy soil?

Another alternative (2) is that the hominins *did* use bone tools to dig into termite mounds, but for another reason. Perhaps for *geophagy*, which does yield micro-nutrients, at least in *Macrotermes* (Seymour *et al.* 2014) but need not entail accompanying termitivory? In southern Africa, *Macrotermes* mounds show enrichment of multiple micro-nutrients compared with *Trinervitermes*, which show none (Mills *et al.* 2009). Neither of these alternatives has been investigated systematically for *Pan*, but chimpanzees *do* dig wells for drinking water in sandbars in riverbeds (McGrew *et al.* 2013), and chimpanzees (Reynolds *et al*. 2019) and humans (Hunter 1993) *do* consume termite earth, without digging, especially from *Macrotermes.*

Wild chimpanzees *do* dig for other social insects, such as stingless honey-bees using tools (e.g. Estienne *et al.* 2017), as revealed by camera trap data that provide both the behavior and its products. Primate archaeological data from unhabituated chimpanzees suggest digging into the nests of army ants (Pascual-Garrido *et al.* 2013). But all such cases seem to be the result of using tools of vegetation, not bone. (No one seems to have recorded the availability of weathered bone as a potential raw material for chimpanzees in nature, but many chimpanzee field projects seem to accumulate a collection of such specimens in the process of research, especially at dry and open sites.)

Captive chimpanzees will use tools to dig for food

Figure 2. Close-up of *Macrotermes* soldiers ('Big Macs'). (Photo taken by Robert O'Malley)

Figure 3. *Macrotermes* sp. Mound, Lui Kotale, DRC. (Photo taken by Linda Marchant)

rewards buried by experimenters in contrived settings (e.g. Motes-Rodrigo *et al*. 2019), but their study made available only woody vegetation for use as tools to dig up fruits. The obvious actualistic experiment to be done might be to give captive chimpanzees a range of raw materials, including bone, horn core, and ivory, as potential tools to do their digging in various substrates, and then to subject the tools used to the same analyses employed by the archaeologists. Thus, the behavior could be matched to the use-wear. An even more comprehensive study also would involve the same raw materials applied to an experimental task involving vertical downward compression into the substrate.

So, my conclusion, subject to correction by better-informed readers, is that the use of chimpanzees to model extinct hominin use of bone tools in termitivory was perhaps over-reaching, and that the topic merits further investigation. A lesson to primatologists is that such modelling of extinct hominids based on extant primates should be done carefully and precisely, that is, with focused etho-archaeology. A more general lesson is to tread carefully into cognate disciplines and to consult colleagues across disciplinary lines.

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Non-lethal handling of a captured duiker by a bonobo (*Pan paniscus*) at Wamba: Implications for prey image in bonobos

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INTRODUCTION

Wild bonobos hunt and consume the meat of small to medium-sized terrestrial mammals such as anomalures (e.g., *Anomalurus derbianus, Anomalurus beecrofti*), forest antelopes (e.g., bay duikers [*Cephalophus castaneus*], blue duikers [*Philantomba monticola*]), and other primates (e.g., galagos [*Galago demidovii*], red-tailed monkeys [*Cercipithecus ascanius*], and wolf guenons [*Cercopithecus wolfi*]) (Fruth & Hohmann 2002; Hohmann & Fruth 2008; Surbeck & Hohmann 2008; Sakamaki *et al.* 2016; Samuni *et al.* 2020). However, there are some differences in hunting and meat-eating behaviors among allopatric bonobo populations (Hohmann & Fruth 2003). As mentioned above, prey consumed by bonobos at some field sites include monkeys and duikers (Fruth & Hohmann 2002; Hohmann & Fruth 2008; Sakamaki *et al.* 2016; Samuni *et al.* 2020). On the other hand, at Wamba, in the Luo Scientific Reserve, Democratic Republic of the Congo, hunting and meat-eating behaviors by bonobos have been infrequent compared to those at other study sites (Hohmann & Fruth 2003; Sakamaki *et al.* 2016), and at this site bonobos have never been observed to hunt for mammals other than anomalures (*Anomalurus* spp.) (Ihobe 1992; Kano 1992; Hirata *et al.* 2010). Moreover, a recent study showed that there was a group preference for duiker or anomalure hunting even in a sympatric bonobo population (Samuni *et al.* 2020).

Some previous studies have described hunting and consuming other mammals that are recognized as food as *prey image* in the *Pan* genus (Boesch & Boesch 1989; Ihobe 1992). Boesch & Boesch (1989) suggested that chimpanzees at Taï Forest, Côte d'Ivoire, have a specialized prey image in which monkeys, mostly colobus, are recognized as food, citing an observation that a juvenile male chimpanzee accidentally caught a blue duiker and handled with it as a toy, not as food. Therefore, these differences of prey profile between and within bonobo populations may likely be affected by prey image per respective population. Environmental conditions also contribute to the prey profile across bonobo populations (Wrangham 1975; Sakamaki *et al.* 2016), which suggests the necessity of studying predator–prey interactions at the specified population level.

Understanding the differences in prey images or prey preference in bonobos may be useful for interpreting the variety of bonobo cultures that previous studies have described (Hohmann & Fruth 2003; Samuni *et al.* 2020). Here, I report the first case of an adult female bonobo at Wamba capturing a blue duiker and carrying it around, alive, for approximately 30 min. This case report is important because it contributes to our understanding of the differences in prey profiles, inter-species interactions, and prey image among allopatric bonobo populations.

METHODS

Observations were made at Wamba, where long-term studies on bonobos have been conducted since 1973 (Kano 1980; Furuichi 2011). At this time, there were three identified and fully habituated groups of bonobos at Wamba (E1, PE, and PW) (Sakamaki *et al.* 2018). In July 2018, the E1 group comprised of 41 individuals, including 12 adult females (parous, or ≥ 15 years old), and 2 adolescent females (nulliparous, 8 to < 15 years old), 8 adult males (≥ 15 years old), and 5 adolescent males (8 to < 15 years old) (age classes were categorized by Hashimoto 1997). An adult female known as Zn, who captured the duiker, immigrated to the E1 group from another group (not PE or PW) in October 2011 and was estimated to be 16 years old in 2018.

OBSERVATIONS

The duiker capture occurred on July 25, 2018, during regular *ad libitum* observations of bonobos in the E1 group. At 6:07 h two local assistants and I found a group of bonobos at the location where they had made their night beds the day before. There were ten adult females, two adolescent females, four adult males, and four adolescent males in this group.

At 6:30 h, while I was observing the bonobos at this location, I heard the shriek of a blue duiker and found that Zn was in a tree, grasping an immature blue duiker (Video 1 available online at http://mahale.main.jp/PAN/2021/002.html). Zn lightly swung the duiker in her right hand for a few minutes. While Zn was in the tree with the duiker, other bonobos watched her from other trees or from the ground, and they attempted to approach her but did not interfere. Zn then left the tree and wandered around on the ground, carrying the duiker, for approximately 30 min. The duiker continued to shriek throughout the incident. Zn did not try to eat the duiker during our observations. Several group members (five adult females, two adolescent females, one adult male, and one adolescent male) followed Zn as she moved about, but Zn seemed to run away from these individuals. During observations, I did not observe any aggressive behaviors (e.g., hit, kick, bite) by Zn toward the captured duiker. At 7:00 h, Zn was

lost from sight. At that time, the two local assistants and I verified the presence of all group members that had been seen at the beginning of observations, with the exception of Zn, one adolescent female, and one adolescent male. When I found Zn again at 8:50 h, she did not have the duiker anymore. There was no blood or duiker fur around her mouth, on her hands, or on her body. During the observations, I did not hear any specific bonobo vocalizations expressing anxiety, stress, or social tension (Hayashi *et al*. 2012; Yokoyama & Yasumoto 2019).

DISCUSSION

In the current case, the female bonobo seemed to manipulate the duiker in a manner that might be described as play, which was similar to the bonobo and chimpanzee behaviors described in previous studies (Sabater-Pi *et al*. 1993; Hirata *et al*. 2001; Carvalho *et al*. 2010). Thus the duiker did not seem to be included in the prey image of bonobos at Wamba, although they captured and toyed with it.

Bonobos at Wamba have been observed in non-lethal interactions with other primates, including mutual grooming between bonobos and red colobus (*Colobus badius*) (Ihobe 1990) and a bonobo carrying the corpse of a red-tailed monkey (Toda *et al*. 2017). In addition, there was a single previous report of bonobos interacting with, but not killing or eating, a trapped blue duiker (e.g., approaching, sniffing, touching) (Hayashi *et al*. 2012). Multiple similar incidents have been observed in the habituated groups at Wamba (N. Tokuyama, personal observation; T. Yokoyama, personal observation). A case report at Lilungu (Ikela), Zaire by Sabater-Pi *et al*. (1993) described three observed incidents of bonobos handling, but not eating, captured primates: an angola colobus (*Colobus angolensis*), and a red-tailed monkey (*Cercopithecus ascanius*). In the case of chimpanzees, at Bossou, Guinea, they captured western tree hyraxes (*Dendrohyrax dorsalis*, order Hyracoidea) and West African wood-owls (*Ciccaba woodfordi*), but did not eat them (Hirata *et al*. 2001; Carvalho *et al*. 2010).

Continuing observations of hunting and carnivorous behaviors among bonobo populations will shed light on the factors that cause local differences in prey images in bonobos. Variations in social and ecological factors (e.g., food availability, overlapped range areas among species, human interference) among field sites might affect the different prey images in bonobos that are part of their local traditions or cultures. This case report will be helpful in confirming the differences in prey images and interspecies interactions among allopatric bonobo populations.

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Use of a novel human object as a masturbatory tool by a wild male chimpanzee at Bulindi, Uganda

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INTRODUCTION

Besides humans, self-stimulation of the genitalia (masturbation) has been documented in many primate species (Dixson 2012; Thomsen & Sommer 2017). Although masturbation by captive nonhuman primates is sometimes considered abnormal or, at least, undesirable behaviour (*e.g.*, Mallapur & Choudhury 2003), masturbation also occurs under natural conditions and may represent a phylogenetically ancient and widespread trait in primates (Thomsen & Sommer 2017). Several studies have reported masturbation in wild male primates living in multimale–multifemale groups where sperm competition occurs (*e.g.*, Temminck's red colobus, *Piliocolobus badius temminckii*; Starin 2004; Japanese macaque, *Macaca fuscata*; Thomsen & Soltis 2004; rhesus macaque, *Macaca mulatta*; Dubuc *et al*. 2013). While the hypothesis that male masturbation functions to increase sperm quality (Baker & Bellis 1993) received support in one study of Japanese macaques (Thomsen & Soltis 2004), masturbation leading to ejaculation was observed rather rarely in most reports, suggesting alternative explanations require consideration (Starin 2004; Dubuc *et al*. 2013).

In chimpanzees, masturbation occurs commonly in captive settings where it has been linked to restricted rearing, which can impede development of species-typical social and sexual behaviour (Kollar *et al*. 1968; Rogers & Davenport 1969; Lopresti-Goodman *et al*. 2013). Masturbation by captive chimpanzees is performed by hand, foot or mouth, against a cage wall or screen, or sometimes using a manipulable object (Shefferly & Fritz 1992). In the wild, object-assisted masturbation occurs in male long-tailed macaques (*Macaca fascicularis)*, which stimulate their genitals using stones (Cenni *et al*. 2020). Such self-directed employment of a manipulable object meets the criteria of an animal 'tool' (Shumaker *et al*. 2011).

In contrast to captivity, masturbation appears to be rare among male chimpanzees in the wild. Male chimpanzees of all ages at Gombe and Mahale, Tanzania, manipulated (or 'fumbled' or 'fiddled' with) their erect penises occasionally, but this was never observed to lead to ejaculation (van Lawick-Goodall 1968; Nishida 1997). Recently, Nakamura (2018) described an infant chimpanzee at Mahale 'copulating' with a discarded fruit wadge, which was likened to a 'sex toy'. Besides this, there seem to be no other reports of wild male chimpanzees using manipulable objects as tools in sexual behaviour.

We observed a wild subadult male chimpanzee at Bulindi, Uganda, using a novel human object—a discarded plastic bottle—as a masturbatory tool. While anecdotal (Ramsay & Teichroeb 2019), this unusual observation raises questions about the function of masturbation in male chimpanzees, and contributes to an understanding of the range in behavioural responses of wild apes to novel objects.

METHODS

Study site

Chimpanzees *Pan troglodytes schweinfurthii* in Bulindi (1°29′N, 31°28′E) were first studied during 2006–2007 (McLennan & Hill 2010) and subsequently from 2012 to the present. They inhabit a human-modified environment comprising fragments of riverine forest amidst farmland and villages (McLennan *et al*. 2020). The chimpanzees feed habitually on agricultural crops and encounter local people on a daily basis (McLennan *et al*. 2019a; 2020). They also encounter discarded human objects, including plastic bottles and other litter items.

The Bulindi chimpanzees use leaf or stick tools in various contexts including foraging (McLennan 2011; McLennan *et al*. 2019b) and hygiene. For example, males sometimes use leaf tools as napkins to wipe their penises after mating (unpubl. data). Bulindi males also handle or inspect their erect penises occasionally (Figure 1), typically after copulation or when females with anogenital swellings are nearby. This behaviour is not accompanied by pelvic thrusts, as occurs during copulation, and has not been observed to result in ejaculation. Thus, it appears similar to penis 'fumbling' described at other sites (van Lawick-Goodall 1968; Nishida 1997).

During the present observation in August 2018, chimpanzees were habituated and observable at distances of ≤10 m (Cibot *et al*. 2019). Community size was 19 including 3 adult and 3 subadult males, 5 adult and 1 subadult females, and 7 immature individuals. The subject of this report is a subadult male named 'Araali'. In 2018, Araali was estimated to be 9-years old (Figure 1). He had descended testicles, an adult-sized penis, and displayed rhythmic contractions during mating, suggesting he was sexually mature and able to ejaculate.

OBSERVATION

At midday on 13th August 2018, we followed a party of 11 chimpanzees to a *Lantana camara* thicket. (*L. camara* is an invasive weed that forms dense thickets that the chimpanzees use for resting and shade). The party in-

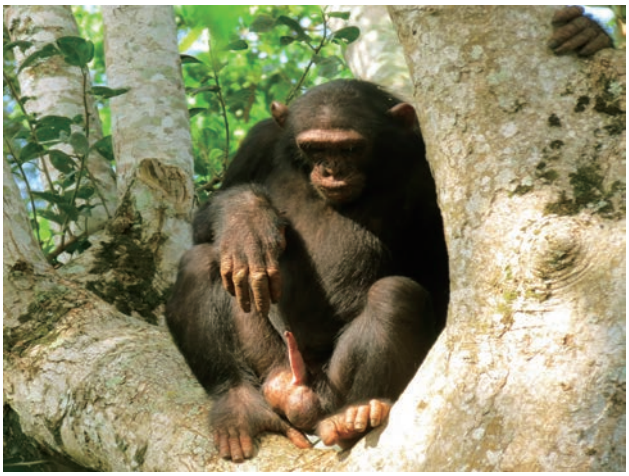

Figure 1. Subadult male 'Araali' in August 2018. The image shows him inspecting his penis after he had mated with an adult female (Photo by Matthew McLennan).

Figure 2. The discarded plastic bottle used as a masturbatory 'tool' by Araali, photographed the following day (Photo by Bulindi Chimpanzee and Community Project).

cluded the alpha male and 3 adult females, none of whom had anogenital swellings. We could hear a chimpanzee manipulating a plastic object under the *Lantana*. At 12:10 h we approached and observed Araali in possession of a medium-sized plastic bottle, which he was 'copulating' with. It is unclear how long he was engaged in this behaviour prior to our approach. The bottle was approximately 1–1.5 L, empty, and without a label or cap (Figure 2); field assistants suggested it was a discarded herbicide bottle of the kind used by local farmers.

We made a 1-min video of Araali's behaviour (Supplementary video available online at http://mahale.main.jp/PAN/2021/003.html). At the start of the recording, Araali had inserted his erect penis into the bottle's open top. For 25 sec he made pelvic thrusting movements into the bottle, which he had positioned flat on the ground in front of him (Figure 3a). Once, he repositioned the bottle after his penis came out. At times he showed a relaxed open-mouth expression (or 'play face'; van Lawick-Goodall 1968). After 30 sec, Araali inspected his erect penis manually before sniffing his fingers. Lifting the bottle, he peered into the open top. He then reinserted his penis into the bottle, which he held in position with one hand while holding a branch with the other (Figure 3b). For the remaining 8 sec of the recording, Araali sat with a play face, apparently with his penis still inside the bottle. Shortly after the recording ended, Araali walked away leaving the bottle behind. It was collected immediately by a juvenile male who, with other youngsters, played with it until we left the chimpanzees at 12:35 h. Therefore, we could not determine if Araali ejaculated into the bottle during the observation. We located the bottle the following evening; however, we did not collect it to test for traces of semen.

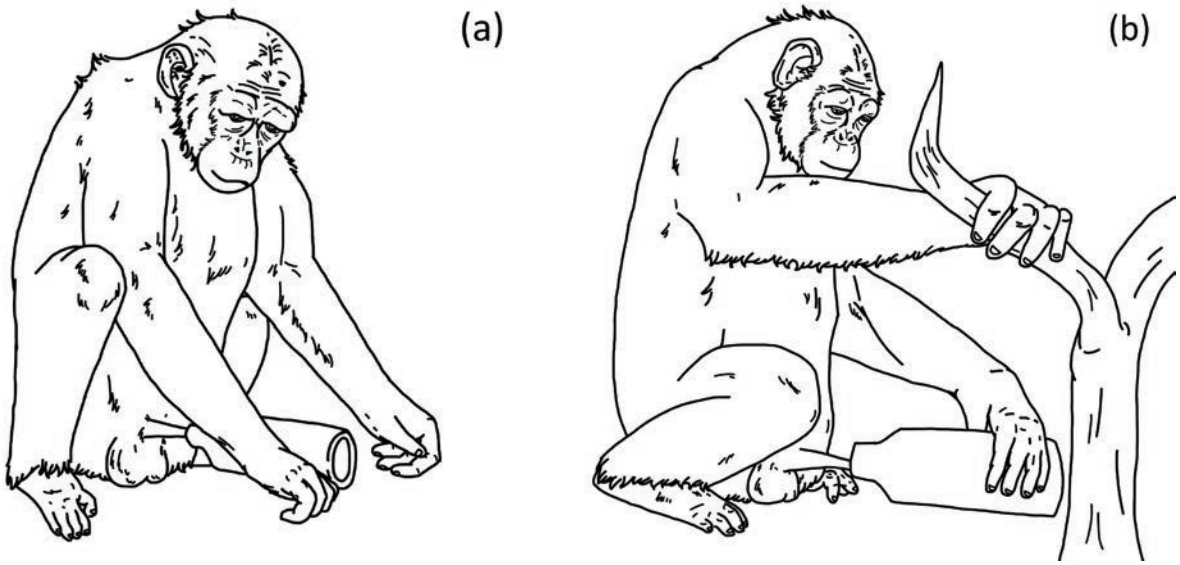

Figure 3 a.b. Illustrations of Araali 'copulating' with the plastic bottle, based on still images taken from video (Illustrations by Kim van Dijk)

DISCUSSION

We observed a wild sexually-mature chimpanzee using a human object as a tool in autoerotic behaviour, i.e. as a 'sex toy'. Our observation shares similarities with a previous report of an infant male at Mahale, which used a fruit wadge as a masturbation tool (Nakamura 2018). Araali's tool-assisted masturbation was further distinct from ordinary penis handling or 'fumbling' by male chimpanzees at Bulindi, which does not involve pelvic thrusting. While we cannot exclude the possibility that Araali ejaculated into the bottle, it seems doubtful: intromission in sexually-mature males is ordinarily short (mean: 7 sec; Nishida 1997), whereas Araali thrust into the bottle for over 20 seconds.

How should Araali's masturbatory behaviour be explained? Male primates in multimale–multifemale social groups, including chimpanzees, may not always be able to copulate because of competition with higher-ranking males. Thus, masturbation could improve semen quality by discarding old sperm (Baker & Bellis 1993). However, no sexually receptive females were present during the observation, making such an adaptive explanation unlikely. In multimale–multifemale groups where sperm competition occurs, males might have neuroendocrine specializations for enhanced sexual arousal and copulatory performance; thus, masturbation could provide a sexual outlet for subordinate males with little or no access to receptive females (Dixson 2012). Although Araali occasionally mated with receptive females, he was subordinate to three adult males. In particular, the alpha male successfully monopolised receptive females (McCarthy *et al*. 2020). Nevertheless, given the rarity of reports of male masturbation in wild chimpanzees, including an absence of reports of masturbation leading to ejaculation (and the lack of evidence for ejaculation in our observation), this ultimate explanation for Araali's behaviour is also doubtful.

Wild great apes including chimpanzees were reported to show generally indifferent or neophobic responses to novel objects (Forss *et al*. 2015; Kalan *et al*. 2019). However, where chimpanzees and other wild primates encounter human artefacts frequently, as at Bulindi, novel human items can elicit interest, leading to object handling and, potentially, novel behaviours (cf. van de Waal & Bshary 2010; le Roux *et al*. 2019). Young chimpanzees at Mahale manipulated and played with long-abandoned clay pots (Matsusaka 2012) and attempted to touch or inspect human belongings (Matsusaka *et al*. 2015). Similarly, the enthusiastic play with the bottle by immature chimpanzees in Bulindi is consistent with previous findings that younger apes are more curious of objects than adults (Ramsey & McGrew 2005; Kalan *et al*. 2019).

Araali's masturbatory behaviour most likely resulted from his motivation to inspect and play with a novel human object. Male chimpanzees exhibit penile erections in various contexts besides sexual arousal, such as food excitement and during some social interactions including play (pers. observ.). The physical properties of the open bottle presumably elicited Araali's autoerotic response, suggesting he recognized its suitability for that purpose. Considering he exhibited a play face while 'copulating' with the bottle indicates his masturbatory behaviour was 'pleasurable' or 'fun'.

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