New observations on chimpanzee accumulative stone throwing in Boé, Guinea Bissau

(*) Corresponding author: Bartelijntje Buys, Foundation Chimbo, Huningpaed 6, 8567 LL Oudemirdum, The Netherlands, E-mail: bbartelijn@gmail.com

Buys, B., van Loon S. en Puijk A.D., Foundation Chimbo, Huningpaed 6, 8567 LL Oudemirdum, The Netherlands

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Abstract: Chimpanzee accumulative stone throwing at trees has been described by Kühl, H.S., Kalan, A.K., Arandjelovic, M., Aubert, F., D'Auvergne, L., Goedmakers, A., Jones, S., Kehoe, L., Regnaut, S., Tickle, A., et al. (2016). Chimpanzee accumulative stone throwing. Sci. Rep. 6: 1-8, but we lack important details about the social and ecological context for this rare behavior. Further observations may enhance future research, as the described observations have not yet been shared in the literature. We analyzed camera trap records from 2010 to 2020 of various research projects conducted in the Boé sector of Gabu Province in south-east Guinea Bissau, West-Africa, to identify ecological and social factors that might potentially influence chimpanzee accumulative stone throwing behavior (on a total of 298 records). From September 2019 until November 2019, we filmed five trees over 48 days to conduct a further exploratory study of this behavior. We discuss the importance of study design when investigating a little-described phenomenon, and the threat posed to chimpanzee populations in West-Africa by the expected expansion of mining activities. More knowledge on chimpanzee accumulative stone throwing is needed as the chimpanzee population is under stress because of increased mining activities in the area. With habitat rapidly being disturbed and destroyed, this population and its rare behavior are increasingly at risk of extermination.

Keywords: camera trapping; chimpanzee accumulative stone throwing; culture; Guinea Bissau; undescribed phenomena.

1 Introduction

Some populations of western chimpanzees (*Pan troglodytes verus* Schwarz 1934) exhibit a particular behavior referred to as 'accumulative stone throwing' (Kühl et al. 2016): individuals often throw stones at specific "focal" trees, generating a loud noise ("*bang*"), accompanied by a pant hoot vocalization (for pant hoot vocalization, see Mitani et al. 1992). The stones accumulate on site, near or inside the base of the focal tree. Chimpanzees either 'hurl' these stones at a tree, 'toss' the stones into a hollow tree cavity and/or between its buttress roots, or 'bang' the stones repeatedly while holding the stone in their hands (Kühl et al. 2016). Occasionally, chimpanzees have been observed drumming the tree with their hands or feet (Buys 2016; Kühl et al. 2016; van Loon 2020; Wenceslau 2014). A sequence of behaviors is often performed in an almost ritual manner, such as staring at the tree, swaying back and forth and an accelerating and increasingly louder *u:hu:*-sound, culminating in a loud scream, up to and including the throwing of a stone and/or hand or feet drumming (Buys 2016; Kühl et al. 2016; van Loon 2020; Wenceslau 2014) (see Supplementary Video 1). This phenomenon was first reported as 'stone drumming at trees by chimpanzees' based on observations by the local population of the Boé sector in the southeastern part of Guinea-Bissau (Goedmakers 2010).

Whilst some ecological and social explanations for this behavior have been proposed (symbolic, communication and male display) (Buys 2016; Kalan et al. 2019; Kühl et al. 2016; van Loon 2020; Wenceslau 2014), we know little about the contextual (nocturnality, rainfall, environment) and social factors that may impact accumulative stone throwing in Boé, such as individuals simultaneously throwing stones and transfer of behavior. Chimpanzees in Boé repeatedly have been recorded engaging in stone throwing in all seasons (Buys 2016; Kühl et al. 2016; van Loon 2020; Wenceslau 2014). Adult chimpanzee males are more frequently recorded throwing stones at trees, but females and juveniles have also been observed exhibiting the same behaviors (Buys 2016; Kühl et al. 2016; van Loon 2020; Wenceslau 2014). Van Loon (2020) found a

correlation between chimpanzee accumulative stone throwing in Boé and non-aggressive intimidating displays and (long distance) communication. Hand and/or feet drumming occurred in one third of the reported chimpanzee stone throwing events. Boé's chimpanzees prefer trees that have higher resonant qualities compared to other trees available in their habitat (Kalan et al. 2019), such as *Ceiba pentandra*, *Cola cordifolia* and *Pterocarpus erinaceus*, *Treculia africana*, *Bombax costatum and Crossopteryx febrifuga*, suggesting their importance for long-distance communicative purposes. Anecdotical evidence suggests that density, distribution and functional diversity of target trees might differ among locations (Buys 2016, supplementary online material). Kalan et al. (2019) reports that only 39 trees out of hundreds of available trees are used for chimpanzee accumulative stone throwing.

A more holistic description of accumulative stone throwing might benefit future research to set up further hypotheses and explain each factor in more detail. Contextual factors such as rain and rocky environments (as pictured in Figure 1) may influence sound transmission, but at the same time play a role in symbolic function. Investigating the social context of stone throwing events is necessary to assess how the behavior functions within the Boé population and for later cross-population (cultural) analyses.

There are both behavioral and conservation reasons to better understand stone throwing. This rare behavior may be a response to the presence of certain acoustic trees and a means of communicating with distantly locating conspecifics (Kalan et al. 2019). Moreover, with chimpanzees and their rich cultural repertoires (Kühl et al. 2019) under threat across their distribution (Carvalho et al. 2021), includes in Boé where mining is a direct threat to chimp habitat, documenting and understanding these rare behaviors may play an even larger role in their conservation (Brakes et al. 2021).

2 Materials and methods

2.1 Study area

The Boé sector is an administrative entity of the Gabu Province in South-East Guinea Bissau, bordering Guinea. Often it is referred to as 'The Boé' or 'The Boé region', cf. the map in Figure 2. It is a remote area of ca. 3000 km^2 of forest-savannah mosaic in the south-east of Guinea-Bissau, West Africa, with an estimated population density of 3,6 human inhabitants per square meter (or a total population of ca. 12,000 people living across 28 villages) (Breider et al. 2016; Wit and Reintjes 1989). The soil is covered by a thick laterite cap of savannah grassland, intersected by secondary and gallery forests of some hundred meters wide and 10 km long (Breider et al. 2016; van der Hoeven 2020; Wit and Reintjes 1989). The mean annual rainfall is 1600–2000 mm, while the rainy season starts in May and ends in October (Catarino et al. 2008; van Steenis 2017). In the savannah edged forests and secondary forests, common trees are *Pterocarpus erinaceus*, *Spondias mombin* and *Parkia biglobosa*, while closer to and within the riparian gallery forests, *Afzelia Africana*, *C. cordifolia* and *C. pentandra* trees become more present (forest types according to White and Edwards 2000) (Catarino et al. 2008; van der Meer 2014; Wit and Reintjes 1989). Large parts of the Boé, being unsuitable for agriculture (Wit and Reintjes 1989), thus remain uncultivated; peanut and rain-fed rice are the most common grown crops in small scale fields (ca. 14609 m^2 on average) (Betel 2020). A rotating slash-and-burn practice is common to increase soil fertility, yet an increasing number of fields are turning into cashew orchards instead of being left abandoned for 3–6 years after being burned (Betel 2020; Temudo et al. 2015).

Figure 1: A focal chimpanzee accumulative stone throwing *Ceiba pentandra* tree in the sacred gallery forest of Capebonde, picture taken by a Bushnell camera trap 7 May 2013 at 15h36 (by J.F.C. Wenceslau, Foundation Chimbo). Big flat rocks are surrounding the tree on which a chimpanzee group may sit and play. Tree diameter at breast height is ca. 3.6 m.

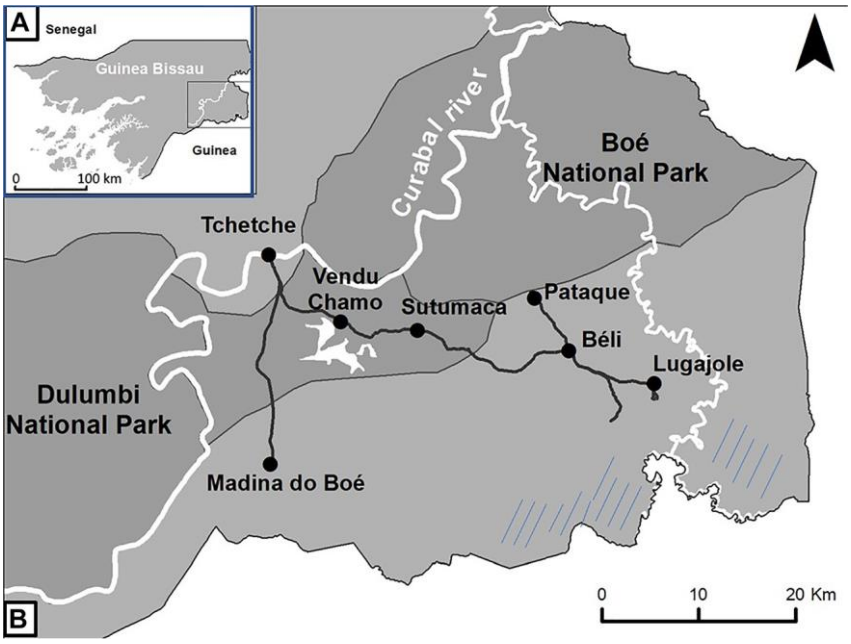

Figure 2: (A) Location of the Boé sector in Guinea Bissau, bordering Guinea. (B) Map of the Boé sector, with main streams (white lines), roads (black lines) and main villages (e.g., Béli, Lugajole) (black dots). The Boé National Park, Dulumbi National Park and the Tchetche Corridor are indicated in dark grey, explored mining areas shaded. Map adapted from Guilherme 2014. Exact camera trap locations are withheld for ethical reasons.

Estimates of Western chimpanzee populations based on line transect counts carried out for the Chimbo Foundation within the Boé sector range between 1000 and 1500 (A. Goedmakers pers. comm.; Nunes van den Hoven 2017). Like other savannah dominated landscapes, highest chimpanzee nest densities might be found in secondary dry – and gallery forests all year round (Nunes van den Hoven 2017; Sousa et al. 2014). In Boé, forests of all kinds have a sacred status, but especially in unlogged sacred gallery forests at the source of streams, human disturbance has been absent for a long time (Ramachandra 2017). Nunes van den Hoven (2017), however, did not find an overall divergence in Western chimpanzee abundance among sacred and non-sacred forests, with and without water, in the Boé region.

Local people have a strong respect for chimpanzees and do not disturb, hunt, or harm them, based on cultural taboos (see Sousa et al. 2017, 2018) for other regions in Guinea-Bissau with similar cultural restrictions. There is anecdotal evidence of chimpanzees harvesting fruits of a baobab tree in the principal village of Béli (see map), and chimpanzees eating oranges in another village, Capebonde, but chimpanzees are not considered crop-raiding species in Boé. Out of 57 crop fields monitored during the rainy season of 2018, only two fields that contained sugarcane (in addition to the most grown crops rice and peanut) had been damaged by chimpanzees (Betel 2020). In undisturbed old sacred forest (Ramachandra 2017; Wit and Reintjes 1989), the density and diversity of focal trees is expected to be higher than other similar habitats (Buys 2016) possibly as a consequence of limited human presence that creates a favorable environment for chimpanzee cultural development (see Kühl et al. 2019 on this topic).

The Boé contains a substantial bauxite mining area near the Guinea border (Figure 2B) and S.A. Bauxite Angola project plans coincide with important chimpanzee habitat (Dias et al. 2019; Wenceslau 2014), biodiversity hotspots, and water sources (Breider et al. 2016; Guilherme 2014; Wit 2011). As of Spring 2021, mining had not begun, but infrastructure had been constructed, including in chimpanzee habitat (Dias et al. 2019).

2.2 The Chimbo Foundation and camera trapping

The Chimbo Foundation (“Chimbo”) is an NGO established in 2007 with the objective of contributing to the conservation and protection of the Western Chimpanzee and its habitat. Since 2007 the organization has worked in the Boé region of Guinea Bissau to strengthen local conservation efforts with students’ research, and working with stakeholders to protect chimpanzees.

A mix of local initiatives, local monitoring (i.e., by 28 village committees), and the research of 50 international students and scientists, has produced a large number of camera trapping events (both videos and photographs) and reports about the Boé region (cf. research results of Chimbo are downloadable on https://www.chimbo.org/steun-ons/onderzoeksverslagen/) from the period 2013 until 2020 analyzed for this manuscript. These deployments were designed to monitor the study area and provide baseline data on fauna diversity, including on Boé chimpanzees. In a first step, we collated and coded all videos out of these recordings that pictured chimpanzee accumulative stone throwing events, resulting in a total of 286 videos. Typically, the sensor level of the Bushnell Trophy cameras (NatureView Cam HD Max, type 119439) was set to “High”, the resolution or video size was 1280 × 720, and video length was 60s. Though frequency varied between studies, generally cameras were checked every three to four weeks.

Next, we collected additional data on each video capture that included chimpanzee stone throwing, including contextual, ecological and social criteria; such as day-night rhythm, seasonality, environment, chimpanzee age and group behaviors. Links to the Supplementary Videos can be found in the Supplementary Online Material.

Thirdly, to counteract data limitations, such as data gaps and unevenly distributed and non-continuous design of the various exploratory projects, each newly recorded behavioral category of stone throwing (Table 1) has then been compared with its relative occurrence five focal trees at different locations in the Boé for 48 days

Table 1: Behavioral categories observed by camera trapping.*

Environmental factors influencing chimpanzee accumulative stone throwing
Rebounding of stones on rocks (see Results Section 3.1.1)
Stone throwing at more than one tree using different sizes of stones (see Results Section 3.1.2)
Stone throwing at night (see Results Section 3.1.3)
Stone throwing in pouring rain (see Results Section 3.1.4)
Transfer of chimpanzee accumulative stone throwing behavior
Stone throwing by an infant (see Results Section 3.1.5) Copying behavior (see Results Section 3.1.6)
Stone throwing by a juvenile and an adult together (see Results Section 3.1.7)
Social interactions of adult males at accumulative stone throwing sites
Male adults repeatedly throwing stones together against the same focal tree (see Results Section 3.1.8)

*All videos were made by a team of independent researchers of Foundation Chimbo in Boé region, Guinea Bissau, during the period 2010-2020. The sensor level of the Bushnell Trophy cameras (NatureView Cam HD Max, type 119439) was set to "High", the resolution or video size was 1280 × 720, and video length was 60s. No exact positions of location are given because of ethical reasons. In the Supplementary Reading Section additional observations can be found on all categories, including a section on particular observations of female chimpanzees at stone throwing sites. Links to the videos are available in text.

in September-November 2019. This allowed us to extract relative frequencies of each behavior. In this reference study, van Loon deployed three cameras at each tree (one to three camera placed at ca. five meters in front and two cameras at both sides of the tree at 10 meters distance). Of the five trees, three were located in primary, riparian gallery forests, and two in secondary forests. The data gathered by van Loon was chosen for a reference study because of all the camera trap studies conducted in Boé to date, this was the most equally distributed and resulted in best availability of continuous data.

All data was analyzed manually through an EXCEL form (Windows 10, Microsoft Software), implementing contextual (e.g., day-night rhythm, rain-no rain weather, group-no group) categories and individual chimpanzee characteristics (e.g., sex and age) in columns to each observation in separate rows, using filters for data readability. Furthermore, particular events were described in detail and camera trap records repeatedly watched and carefully analyzed.

3 Results

We analyzed 289 camera trap records of chimpanzees throwing stones at focal trees in Boé out of a data set from the Chimbo Foundation, combining various research projects in Boé in the period 2010-2020. Newly described phenomena out of this dataset were categorized as chimpanzee stone throwing at night, in pouring rain, in rocky environments, by infants, by adults and by juveniles together. We further describe the use of more than one size of stone while stone throwing, or more than one tree in one stone throwing event and the use of focal trees in rocky environments (as pictured in Figure 1). Finally, observations regarding transfer of behavior, such as juveniles exploring stone throwing or directly copying the behavior, are added to the list. An example of each new chimpanzee stone throwing phenomenon is described in detail below and summarized in Table 1. Links to the Supplementary Videos of each new described behavior are given in the Supplementary Online Material.

3.1 Categories of contextual and ethological factors

Firstly, we describe contextual and ecological factors potentially influencing chimpanzee accumulative stone throwing behavior.

3.1.1 Rebounding of stones on rocks

On 28 April 2013 at 13h27, we recorded a chimpanzee throwing a stone at a focal tree standing in a rocky environment (Figure 1). After the stone hits the tree, the stone rebounds on a rock and produces a second, distinctive sound. We hear reverberating of the sound within the rocky environments (see Supplementary Video 2).

3.1.2 Stone throwing at more than one tree using stones of different sizes

On 23 June 2015 at 07h32, we recorded a male shaking leaves and bushes and banging a stone at a second tree after having thrown some at the main focal tree of the stone accumulated site. Within this event he uses two stones of different sizes. He first throws the biggest stone, then the smaller stone, then again the biggest stone at the focal tree. The different stones are thrown with similar intensity, gesture and at the same spot on the buttress tree. The larger stone produces a duller sound (i.e., a sound with a lower frequency) than the smaller stone. He then runs up to the second tree and bangs it with the smaller stone (see Supplementary Video 3). The sound produced by the different trees and stones is different, with the larger objects producing duller sounds than the smaller ones.

3.1.3 Stone throwing at night

A first series of observations was made on 20 July 2015 a non-moonlit night (15% illumination, waxing crescent

moon). A young adult male was observed throwing stones at a focal tree at 03h46, again at 03h49 and once again at 05h20 (see Supplementary Video 4). Only after the first throwing event accompanied by a pant hoot vocalization, can screams of other chimpanzees be heard in the distance. The individual appears to be searching for accumulated stones by touch. The individual was also scratching and yawning prior to and after stone throwing events, but it is not clear whether within this context these should be regarded as displacement activities. He was sitting down near the tree and went out of camera view between 03h49 and 05h20. After his last stone throw, he began hanging on ('hugging') the tree, then he fell asleep in front of the tree for 10 minutes, after which he left the scene.

3.1.4 Stone throwing in pouring rain

On 23 August 2015 at 18h07, we recorded an adult chimpanzee throwing a stone at a focal tree while it was raining heavily (see Supplementary Video 5).

3.1.5 Stone banging by an infant

Secondly, we describe specific records of infants and juveniles throwing stones at chimpanzee accumulation sites in relation to the transfer of this cultural behavior.

2 April 2015 at 8h38: we recorded an infant jumping off the back of a female adult that was passing a focal tree with accumulated stones. The infant grabbed a small stone at the base of that tree and banged it once on the tree adjacent to the focal tree. No prior footage of stone throwing by any other chimpanzee was recorded that day. Moreover, there did not seem to be any prompt to provoke this behavior except the presence of the accumulative stone throwing spot itself. The infant was thus not directly copying the behavior of an adult at that moment. (See Supplementary Video 6).

3.1.6 Copying behavior

23 May 2018 at 15h46: an adult male is showing accumulative stone throwing behavior. In the building-up phase prior to throwing, a juvenile climbs into a small tree next to the focal tree. Then the juvenile drums his feet at the moment the stone is thrown by the adult. The adult male leaves the camera view directly after stone throwing, and a few seconds (14 s) later, the juvenile comes out of the tree and throws a stone at it before leaving as well (but in the opposite direction of the adult male). (See Supplementary Video 7).

3.1.7 Stone throwing by a juvenile and an adult together

17 July 2015 at 07h21: an adult male and juvenile chimpanzee are throwing stones together; first the juvenile throws a stone, then the adult, then they both run away. (See Supplementary Video 8).

3.1.8 Male adults throwing stones together at the same focal tree

Thirdly, we describe an example of an event in which male adult chimpanzees throw stones together at the same focal tree.

4 November 2019 at 08h51: three adult male chimpanzees are recorded near the same tree at the same time by three camera traps positioned at different sites around the tree. One male is feet drumming, at almost the same time another adult male is stone drumming on another side of the tree. Both actions are accompanied by pant-hoot vocalization, almost synchronically. They walk away. A third adult male has been recorded watching the scene and walking away after it, in the same direction as the other two (see Supplementary Video 9a-c).

3.2 Other observations and categories

[Correction added after online publication 29 April 2022: heading 3.2 was added.]

More examples can be found in the Supplementary Online Material, which also adds observations of females and juveniles that are not directly copying the behavior (already described in Buys 2016; Kühl et al. 2016; Wenceslau 2014).

The above newly described observations were investigated for relative frequency within a subset of the reference dataset of van Loon, who filmed five focal trees at different locations in Boé over 48 days in September 2019-November 2019, resulting in 77 chimpanzee stone throwing records. Each described phenomenon is represented as a different orthogonal category within the histogram of Figure 3. Most of the records showed adult males throwing stones to focal trees (76 of 77 accumulative stone throwing events) during day time (73 of 77 accumulative stone throwing events). Four times accumulative stone throwing occurred during the night, and four times in rain. Females and infants were not recorded stone throwing at a tree and juveniles only once (but not directly copying the behavior of an adult). Within this subset of data,

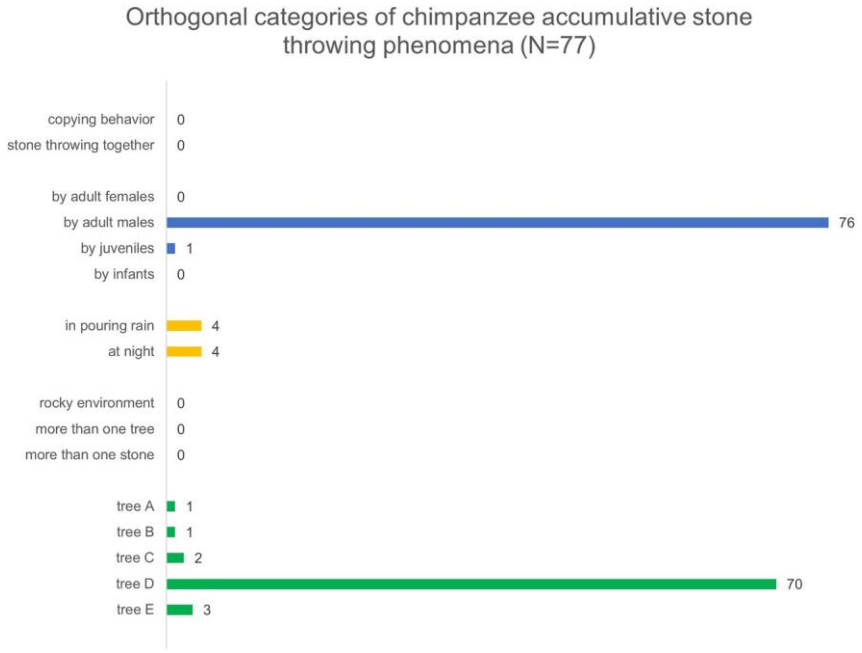

Figure 3: Histogram on orthogonal categories of accumulative stone throwing behavior relative to a small reference study targeting five focal trees at different locations in Boé, Guinea Bissau, over a period of 48 days in September-November 2019. Bars indicate the number of chimpanzee accumulative stone throwing observations: at the different trees (green), at nighttime and in pouring rain (orange), and by which actors (blue). Zero observations indicate described phenomena or situations that have not been observed in the latter reference study.

there were no observations of chimpanzees using different stones and trees while stone throwing, or chimpanzees (adults and/or juveniles) throwing stones together at the same tree; nor a focal chimpanzee stone drumming tree within a rocky environment. 70 of the 77 chimpanzee accumulative stone throwing events were recorded at one particular tree of the reference study, while the other seven observations were recorded at the other four trees included in the study (Figure 3).

4 Discussion

The observations described in the previous section review a variety of situations with a variety of actors in which chimpanzee accumulative stone throwing occurs. This variety appears not to be unusual but is part of the phenomenon itself (see Supplementary Online Material). Both night and rain have influence on behavior and on sound transmission, as does physical environment (Bradbury and Vehrencamp 1998; Clink et al. 2020; Lengagne and Slater 2002; Link et al. 2011; Luther and Gentry 2013; Staicer et al. 1996) and intrinsic- and social context (Gilby et al. 2006; Staicer et al. 1996; Wakefield 2013). Although a majority of observations show chimpanzee accumulative stone throwing by adult males in dry weather during the day (cf. Kühl et al. 2016: 61 of 63 reported cases); we observed chimpanzee stone throwing including at night, in pouring rain, and in group. Moreover, we found evidence of early transfer of behavior (copying behavior of juveniles, and stone throwing by a juvenile and an adult together). Sharing observations is therefore crucial for future research.

When investigating chimpanzee accumulative stone throwing behavior, a lot of the observed variability will coincide with the experimental set-up and the further analyses used to describe the data as illustrated in our reference study in which 70 out of 77 observations appeared to become from the same tree. Therefore, "*we must remember that what we observe is not nature itself, but nature exposed to our methods of questioning*" as pointed out by Heisenberg (1958, cit.). We cautiously expect that a similar variability of phenomena accounts for different kinds of focal trees, the context they are standing in and how frequently they are used for stone throwing (Buys 2016; Kalan et al. 2019). Individual chimpanzees (and probably also groups) may influence the dataset and recorded observations by returning to a particular tree and/or showing the same behavioral traits when engaged in stone throwing (Buys 2016; Kühl et al. 2016; van Loon 2020). For example as appears in the Supplementary Online Material there are observations of a single elderly female who was the only individual to return to one particular tree for stone throwing during an entire month of recording.

When the study design is carefully chosen and adds to the interpretation of the results and therefore of this behavior, we might find answers to the concrete questions and hypotheses we propose. We might find answers concerning sound propagation (Kalan et al. 2019), drumming and display related traits (van Loon 2020), but other aspects, such as ritual function, are especially difficult to detect and measure. Chimpanzees are known to have a highly intelligent life and social culture (Fouts and Mills 1997; van Lawick-Goodall 1968, Whiten et al. 1999), including having a sense of aesthetics, such as balance and

form (Casti et al. 2019), which might relate to the visual appearance of the focal trees with (sometimes) piles of accumulative stones (such as stone cairns used by humans in other West-African regions, Lentz and Sturm 2001 referred to in Kühl et al. 2016), and senses of rhythm (Dufour et al. 2015) when using objects for sound production.

Future research is needed to improve our knowledge of chimpanzee accumulative stone throwing, what drives this behavior, what is its purpose, how it is affected by social and ecological factors, and how the transfer of behavior occurs (Buys 2016; Kühl et al. 2016; Kalan et al. 2019). This understanding will be important to achieve the long-term preservation of Boé chimpanzees and their unique culture. The chimpanzee habitat in West Africa is currently highly threatened by increased mining activities, demographic developments, and globalization (Heinicke et al. 2019; IUCN SSC Primate Specialist Group 2020). Mining will not only increase deforestation but will also increase water pollution and disturbance by human activities during day and night time. The Boé is considered to be an important region for Western chimpanzee conservation (IUCN SSC Primate Specialist Group, 2020). The many riparian gallery forests might have provided a network of glacial micro-refugia for chimpanzees since the last Interglacial (120,000 BP) and will provide shelter at drier periods in times of change (Barratt et al. 2021, pers. com.). Moreover, extractive industry activities usually attract people from outside the region that may not have the balanced relationship with chimpanzees that local people have, increasing the possibility of negative human-wildlife interactions and poaching. Local people in Boé have been protecting chimpanzees, chimpanzee culture, and the chimpanzee habitat for centuries through local taboos, and will continue to play a crucial role in chimpanzee conservation. Both wildlife and humans depend on the products and services of the ecosystems of the region. Furthermore, the preservation of this authentic habitat and environment is essential to preserve this chimpanzee behavior.

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Supplementary Material

New observations on chimpanzee accumulative stone throwing in Boé, Guinea Bissau

Bartelijntje Buys et al.

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(A) Supplementary videos

All videos were made by a team of independent researchers of Foundation Chimbo. The sensor level of the Bushnell Trophy cameras (NatureView Cam HD Max, type 119439) was set to "High", the resolution or video size was 1280 x 720, and video length was 60s. No exact positions of location are given because of ethical reasons. Links to the Supplementary Videos (of a private and hidden YouTube channel) are given below:

Supplementary Video 1: https://www.youtube.com/watch?v=JtEFKZO9cEo&feature=youtu.be

Supplementary Video 2: https://www.youtube.com/watch?v=DTTICMssZ5k

Supplementary Video 3: https://www.youtube.com/watch?v=WMxN9-vpDbg

Supplementary Video 4: https://www.youtube.com/watch?v=YG7WUpiTUFY

Supplementary Video 5: https://www.youtube.com/watch?v=K_haMUuuU24&feature=youtu.be

Supplementary Video 6: https://www.youtube.com/watch?v=rbFZXdTcJX4&feature=youtu.be

Supplementary Video 7: https://youtu.be/cT-7rl0EyEc

Supplementary Video 8: https://youtu.be/ujo9RdafLl4

Supplementary Video 9a (*): https://youtu.be/COey4c1glYY

Supplementary Video 9b (*): https://youtu.be/5c1y0VtRdh0

Supplementary Video 9c (*): https://youtu.be/3cfHA9ZyZ1g

(*) Recorded by S. van Loon, Foundation Chimbo.

(B) Supplementary Reading Material

1. ECOLOGICAL FACTORS INFLUENCING STONE THROWING BEHAVIOR

Supplementary Table 1: Additional observations on ecological factors influencing chimpanzee accumulative stone throwing.

Camera trap observations (*)

1.1. Example of a second observation of accumulative stone throwing at night

Description:

On the 12th of April 2019 a series of remarkable chimpanzee accumulative stone throwing at night was recorded at a location other than the one reported in the manuscript: once at 03h35, once at 03h39, once at 05h35, once at 05h38 and once at 06h19. Response of distant (i.e. out of view) yelling chimpanzees can be heard after the first and second throwing events. The stone thrower is (again) an adult male, who is drumming his feet in the building up phase just before the throwing of the stones during the first and second stone throwing events. After each stone throwing event (bar the second one) he sits down on a rock close to the tree, and after the stone throwing events recorded after 5h00: scratching himself and then sitting crouched down with his arms around his knees and his eyes closed.

Video link:

https://www.youtube.com/watch?v=OPv6juxkBhg&feature=youtu.be

1.2. Example of a second observation of accumulative stone throwing in pouring rain

Description:

The behavior of accumulative stone throwing in pouring rain described in the article in Mammalia was confirmed by a second record on the 26th of September 2019, at 7h31. In the latter observation, the chimpanzee quickly comes and goes within camera view to throw the stone.

Video link:

https://www.youtube.com/watch?v=DROvWuAhyQU

1.3. Rolling a stone until it hits a rock

Description:

On the 11th of February 2020, a male adult chimpanzee was recorded to drum his feet on a focal tree, to shake some bushes, to drum his feet again and rolling a stone from the tree until it hits a rock. A clear noise can be heard when the stone bounces on the rock.

Video link: https://www.youtube.com/watch?v=w9QAxKQpqPU

1.4. Choosing stones of different sizes

Description:

On the 1st of June 2019, at 09h00, an adult chimpanzee is sitting on a buttress root of a focal tree when a camera trap starts recording. About 40 seconds later, he stands up and he is possibly searching for a stone near the focal tree for stone throwing. We observe him touching and lifting three different stones, after which he walks with the last and biggest one up to the tree. At that time, a juvenile is also throwing a smaller sized stone towards him, that he does not take. The recording ends just before any stone throwing occurs.

Video link:

https://www.youtube.com/watch?v=kwBRK-hsbD8

(*) All videos were made by a team of independent researchers of Foundation Chimbo. The sensor level of the Bushnell Trophy cameras (NatureView Cam HD Max, type 119439) was set to "High", the resolution or video size was 1280 x 720, and video length was 60s. No exact positions of location are given because of ethical reasons. Links are given to the supplementary videos.

Box 1: Discussion on ecological factors influencing chimpanzee accumulative stone throwing.

Discussion

Our observations confirm that chimpanzee accumulative stone throwing may happen during night time, in pouring rain and in rocky environments. Ecological and time related factors may thus influence chimpanzee stone throwing behavior and the propagation of sound. This adds to the effects of individual variations in strength and tactic, the size of the stone, the resonance qualities of the trees (Cf. Rossing 2007 on acoustic principles).

A pan-African study by Tagg et al. (2018) revealed that nocturnal activity of chimpanzees is more substantial than previously thought. Nocturnal activity included anecdotal observations of pant hoot vocalization and hand or feet drumming (Hicks 2010; Piel 2018; van Lawick-Goodall 1968; Zamma 2013), and is possibly unaffected by moonlight (Tagg et al. 2018). During true night (> 30 min after sunset or before sunrise), Tagg et al. (2018) recorded chimpanzee 'movement' behaviors (such as running and walking) (80,9%), followed by observations of 'on location' behavior (such as standing, sitting, climbing in a tree) (14,9%), while 'social' behaviors (playing, grooming and displaying) and 'feeding' behaviors occurred only rarely in 235 nocturnal observations. Interestingly, Tagg et al. (2018) did not observe chimpanzee activity during true night in the Boé region. The night observations of chimpanzee accumulative stone throwing may be rather rare. Van Loon (2020, unpublished data) recorded four accumulative stone throwing events during true night between 20h27 and 21h06 out of a total of 92 stone throwing records, during a consistent 4 month (September – November 2019) camera trap survey at 5 different drumming trees at different locations in the Boé area.

Moreover, the survey of van Loon (2020, unpublished data) observed only two records of chimpanzee accumulative stone throwing in pouring rain (on the 16th of November 2019 at 15h33 and 15h56). Data of Sommer et al. (2004) suggested that chimpanzees tend to make fewer sounds during rainier months. In Boé, the rainy season generally starts in May and ends in October with a mean annual rainfall of 1,600-2,000 mm (Catarino et al. 2008; van Steenis 2017). Further research is needed to determine if chimpanzees use focal trees with high resonance timber for propagating sound especially during periods of heavy rainfall when stone drumming for communication.

Surrounding rocks might strengthen the echo or sound propagation of a stone throwing event (Cf. Rossing 2007 on acoustic principles). In addition, the sound of a stone falling on a rock after being thrown by a chimpanzee produces another distinctive sound, which hypothetically might have its own communicative purpose (being or not being an "accidental byproduct" of accumulative stone throwing). Van Schijndel (unpubl. 2012) attributes the presence of occasional marks on large rocks in Boé to possible chimpanzee stone throwing.

Except for adding sounds of stones falling or thrown on rocks, different trees may produce different resonant timbres (Kalan et al. 2019) and additive sounds if more than one tree is involved in the stone throwing event whether for communication or display purposes. Buys (2016) also describes chimpanzee accumulation sites where more than one tree has clear marks of chimpanzee stone throwing events.

The size of the stone has an impact on the sound quality when thrown to a tree, with larger and heavier stones presumably producing more intensive sounds with bigger resonance than smaller stones (Cf. Rossing 2007 on acoustic principles). More research is needed to reveal clear answers about a deliberate selection of stones (size and quality) by chimpanzees.

2. TRANSFER OF CHIMPANZEE ACCUMULATIVE STONE THROWING BEHAVIOR

Supplementary Table 2: Additional observations related to juvenile chimpanzee stone throwing.

Camera trap observations (*)

2.1. Juveniles and infants exploring accumulative stone throwing and focal trees

Description:

7 October 2019 at 17h19: a second observation was made, of a female adult chimpanzee that is carrying an infant and passing a focal tree, followed by a juvenile. The juvenile stops, goes to the tree, grabs a stone, sits down for some seconds, and then continues in the direction of the others without actually stone throwing. (See video 1). 14 May 2018 at 8h47: at the same tree a juvenile was pictured alone, handling the stones by grabbing different stones and rolling them over the ground (See video 2); 9 July 2019 at 12h50: a juvenile is banging and twice throwing stones, hand and feet drumming and knocking gently at it buttress roots. (See video 3).

24 December 2019 at 17h39: a small juvenile is pictured near the focal tree, holding a stone in its hand. He repeatedly, softly bangs the stone to the tree at different spots (4 times in total), almost without producing sound. He must be of a young age: he is still balancing on his two feet when standing upright and swaying one hand above his head to bang the stone. He smells

at the bark. When he leaves, he jumps on a buttress root with both feet. A female adult then comes into view and leaves the scene as well. (See video 4).

3 May 2019 at 13h27: an infant was observed drumming with his feet and hands repeatedly, walking up a buttress root of a focal tree. An adult and juvenile were near the juvenile, but did not show any drumming or accumulative stone throwing related behavior. (See video 5).

Video links:

1) https://www.youtube.com/watch?v=gn5JGR_xn1o
2) https://www.youtube.com/watch?v=hdRPLSUW7Hg
3) https://www.youtube.com/watch?v=0S7ZZzs3sLo
4) https://www.youtube.com/watch?v=jzb8S5k2oeY
5) https://www.youtube.com/watch?v=UY1uvjgz9RM

2.2. An example of another observation of copying behavior of accumulative stone throwing by juveniles

Description:

27 May 2019 at 8h37: an adult male has thrown a stone to a focal tree and gets directly out of view. Less than a minute later (46 s) a juvenile comes into view and throws a stone to the tree as well.

Video link:

https://youtu.be/tlnqvhF0lH8

2.3. 'dominance' behavior of juveniles and adult males towards (other) juveniles

Description:

9 July 2019 at 12u51: a juvenile chimpanzee, who is exploring a focal tree by a/o drumming his feet and throwing a stone, runs away as soon as a big male arrives. The big male then abruptly throws a stone towards the tree. He does not sway, nor uses pant-hoot vocalization or any other behavioral sequence that is often recorded prior to stone throwing events. (See video 1).

14 May 2018 at 8h45: a juvenile chimpanzee is chasing away another juvenile, who was just about to grab a stone near a focal tree, by throwing a stone towards him and taking a position on the buttress root of the tree. (See video 2).

Video links:

1) https://youtu.be/JFtCX3xVwDA
2) https://youtu.be/kLV0a7D2Yhs

(*) All videos were made by a team of independent researchers of Foundation Chimbo. The sensor level of the Bushnell Trophy cameras (NatureView Cam HD Max, type 119439) was set to "High", the resolution or video size was 1280 x 720, and video length was 60s. No exact positions of location are given because of ethical reasons. Links are given to the supplementary videos.

Box 2: Discussion on juvenile chimpanzee stone throwing.

Discussion

Juveniles are recorded playing around focal trees, and to explore and to copy accumulative stone throwing behavior. (Juvenile chimpanzee accumulative stone throwing has been mentioned by Buys (2016), Kühl et al. (2016) and Wenceslau (2014)). Despite the few observations made of intimidating behavior towards stone throwing juveniles, Buys (2016) also describes juveniles playing near focal trees within large (family) parties that are sitting and grooming near the foot of the tree, even when adults are throwing stones.

Hence, it is beyond the scope of this note to discuss copying versus learning behavior in detail, yet we refer to the experiments of Tomasello et al. (1987) and Call et al. (2005), and the references herein, which address observational learning of tool-use and social learning of chimpanzees, stating that chimpanzees have greater ability to learn the function of a tool when observing adults, rather than imitating the behavior itself, but tool-use is somehow culturally transmitted (Tomasello et al. 1987, cf. also Boesch 1996). Interestingly, Persson et al. (2018) highlight spontaneous imitation behavior of chimpanzees and its importance for play, social and communicative functions. Accumulative stone throwing might be regarded as tool-use for a social-communicative function which is transferred over generations.

It is suggested that chimpanzees return over generations to the same trees to throw stones at them, based on local knowledge as well as the longevity of certain focal trees. In Boé, only some giant kapok trees (Ceiba pentandra) (that may live for centuries when fully grown (dr. C. Woodward, pers. com.)) show frequent, fresh and old wounds of stone throwing events (indicated by outgrown bump formations of tree bark), while similar giant kapok trees standing nearby do not (Buys 2016). The above described observations show that juveniles and even infant chimpanzees are attracted to existing accumulative stone throwing spots, for play, exploration and stone throwing, even if adults are not visible on the (subsequent) records. If chimpanzees return over generations to the same trees to throw stones, this might have important implications in terms of understanding the meaning of 'ritual' in the larger sense.

3. SOCIAL INTERACTIONS OF MALE CHIMPANZEES

Supplementary Table 3: Additional observations of social interactions of male chimpanzees when stone throwing.

Camera trap observations (*)

3.1. Additional observations of male chimpanzees throwing stones together

Description:

7 November 2019 at 8h32: one adult male throws a stone at the focal tree and drums with his feet. He sits down for some seconds (20s), and another adult male comes in sight. At 8h33 the newly arrived male throws a stone and drums with his feet, after this he stays near the main stone throwing spot in front of the tree, sitting on a rock. At the same time the other (first) chimpanzee is stone throwing at the other side of the tree and then quickly runs away. The stones are thrown almost synchronously, as is the case for the pant-hoot vocalization of both. At 8h34 the newly arrived male throws a stone, again accompanied with pant-hoot vocalization and drums his feet afterwards against the tree. (See video 1 a-c).

2 December 2019 at 7h29: four adult males are passing a focal tree; three cameras are recording from different angles what happens around the tree. The last two adults throw stones to the tree when passing by. They each throw at the tree from different sides, but almost synchronically, accompanied by pant-hoot vocalization. One of the two chimpanzees also drums his feet onto the tree after stone throwing (end of record). (See supplementary video 2 a-e).

Video links:

1 a) https://youtu.be/jMl01hLHrKo
b) https://youtu.be/jMl01hLHrKo
c) https://youtu.be/jMl01hLHrKo

2 a) https://youtu.be/XHtSAgmxlfY
b) https://youtu.be/Wzg1-jUhLwc
c) https://youtu.be/pYim2sSdgbs
d) https://youtu.be/nxhfVFXSXJI
e) https://youtu.be/xwsQniF-r4Y

(*) Videos made by Sem van Loon, Foundation Chimbo.

3.2. Male adult chimpanzees grooming each other with erected penis after (accumulative) stone throwing together

Description:

Three of these male adult chimpanzees were also recorded grooming each other with erected penis near the foot of the same focal tree on 2 December 2019 at 7h45, after stone throwing together at 7h29. (See above).

Video links:

a) https://youtu.be/qBOmSlfgItw
b) https://youtu.be/F6c44BQAVCE
c) https://youtu.be/bICuq2gwI20

Videos recorded by Sem van Loon, Foundation Chimbo.

3.3. Male adults showing aggression towards other male adults that are throwing stones

Description:

18 June 2015 at 16h31: we observed an individual male throwing a stone at a focal tree; thereafter a bigger adult male chased away the first individual by jumping onto the tree directly after the drumming event of the first individual. (See video 1).

12 December 2019 at 10h36: an adult male chimpanzee is recorded standing near a focal tree. A second adult male walks towards the tree, screaming, showing his teeth, and then throws a stone. The first chimpanzee that stood near the focal tree jumps up and down, screams as well, showing his teeth, throws a stone against the tree at the same spot where the second chimpanzee had just thrown a stone, and is screaming again, showing his teeth, staying in front of the tree. It is not clear whether other male chimpanzees are also involved in this display of aggression, or if the same male adults are running around the focal tree after stone throwing, screaming and showing their teeth (See video 2).

Video links:

1) https://www.youtube.com/watch?v=cjrLC6iR29I&feature=youtu.be

2 a) https://youtu.be/HtG31RCNTXY
b) https://youtu.be/olFcjZedtJE

Videos 2 a-b recorded by Sem van Loon, Foundation Chimbo.

3.4. Response of drumming and stone throwing events

Description:

2 November 2019 at 12h36: an adult male drums his feet against a focal tree of a stone accumulation site, accompanied by pant-hoot vocalization. Another adult male sits nearby. Directly after the drumming event, screams and yells of a party of chimpanzees are heard in the distance (See video 1 a-c). The two males respond by screaming a few times. After one minute they both run away in the same direction out of camera view.

3 December 2019 at 7h42: a male chimpanzee communicates vocally with another chimpanzee out of view at the moment and just after the stone throwing event. The answer-response calls are repeated three times, involving short screams and yelling (it only last for 5 seconds). (See video 2 a-c).

31 October 2019 at 10h57: a party of six adult chimpanzees, males and females with at least one female carrying an infant at her belly, are passing just in front of a focal tree. Vocals (incl. screams) of other chimpanzees are heard in the distance. A big male stays a little behind, and throws a stone against the tree while screaming. At the moment of the stone-throwing event the chimpanzees in the distance are quiet, but just after the stone is thrown, responses are heard. The stone thrower sits still for some seconds, it appears probable he is listening, then he follows the others out of camera view. (See video 3 a-b).

Video links:

1 a) https://youtu.be/VE7qxEXMi2U
b) https://youtu.be/nLqNUsF_bac
c) https://youtu.be/yppCLgdcMtQ

2 a) https://youtu.be/71HuB7lkCfw
b) https://youtu.be/meexYedClH8
c) https://youtu.be/UPmYCqwu598

3 a) https://youtu.be/9s-MdipyvYI
b) https://youtu.be/h7rBP9Dl5-w

Recorded by Sem van Loon, Foundation Chimbo

(*) All videos were made by a team of independent researchers of Foundation Chimbo. The sensor level of the Bushnell Trophy cameras (NatureView Cam HD Max, type 119439) was set to "High", the resolution or video size was 1280 x 720, and video length was 60s. No exact positions of location are given because of ethical reasons. Links are given to the supplementary videos.

Box 3: Discussion on social interactions of male chimpanzees.

Discussion

The observation of the same adult males repeatedly throwing stones together at the same focal giant kapok tree is striking and might add to our understanding of this phenomenon in a social-hierarchical context. Furthermore, three of these male adult chimpanzees were also recorded grooming each other afterwards with erected penis near the foot of the tree. These particular observations were not yet previously recorded, simply because camera trap design might have been limited both in time and space. We expect that camera traps positioned in different angles around other giant focal trees in sacred forest in Boé possibly may give similar results in future studies. Buys (2016) describes more than once focal trees with clear marks of chimpanzee stone throwing at different sides of the tree.

Two of the described videos in this supplementary reading section indicate aggressive behavior among male chimpanzees. Van Loon (2020) found a high occurrence of male intimidating display related traits when observing chimpanzee accumulative stone throwing events, however, mostly with a non-aggressive character such as pant-hoot vocalization, piloerection, bipedal standing, swaying, and in some cases penis erection and leaf clipping (branch shaking has been previously reported by Buys 2016). We here include the fact that showing power is implied when throwing big stones. Van Lawick-Goodall (1968), describes the role that male displays play in achieving and maintaining social status, often consisting of visual signs to conspecifics. The function of (buttress) drumming in male displays for establishing dominant-subordinate relationships is described in Riss and Goodall (1977); although drumming might also be used as response to neighbors and/or foreign chimpanzees and intruders (cf. Herbinger et al. 2009; McLennan and Hill 2010). We illustrated this with clear examples of communication and/or sound production to out-of-view chimpanzees at stone throwing events that respond to the drumming behavior (cf. e.g., Boesh 1991; Crockford and Boesh 2003, 2005; Herbinger et al. 2009; McLennan and Hill 2010).

Hand and feet buttress drumming on trees by chimpanzees is far better understood than accumulative stone throwing (cf. Arcadi et al. 1998, 2004; Boesh 1991; Babiszewska et al. 2015; McLennan and Hill 2010), and might reveal long-distance information about the relative position of chimpanzees to other individuals and/or parties in time and space (up to including the behavioral state of the performer: travelling, eating, resting etc.). Moreover, van Loon (2020) found not only a strong relationship of non-aggressive intimidating male display traits and accumulative stone throwing, but also a high similarity to hand and feet buttress drumming because of the shared non-aggressive male display related traits.

We advocate for a stronger incorporation of field visits, sound records, detailed ecological data (such as habitat, time, type of tree), chimpanzee social structure and territorial boundaries in future research. Camera surveys will benefit from more and higher resolution cameras positioned in different angles and distances at stone accumulation sites and longer recording times - to record and identify the chimpanzee' personalities and responses. Sharing observations is crucial in this preliminary phase, because it influences study design and the formulation of hypotheses.

4. PARTICULAR OBSERVATIONS OF FEMALE ADULT CHIMPANZEES AT CHIMPANZEE ACCUMULATIVE STONE THROWING SITES.

Supplementary Table 4: Additional observations of female adult chimpanzees at chimpanzee accumulative stone throwing sites.

Camera trap observations (*)

4.1. An elderly female to be the only one to repeatedly throw stones at a particular tree in December.

Description:

December 2015: we recorded a female repeatedly throwing stones against the same tree on four different occasions: on 12 December at 09h20 and at 17h32; and on 13 December at 15h44; and on the 18th at 13h37. During the entire month, she was the only individual recorded to throw stones at that particular tree. In each event, she sat down for several seconds on a large buttress root just after stone throwing. Typical display related traits can be observed when she is performing accumulative stone throwing behavior such as bipedal standing, piloerection, swaying and pant-hoot vocalization.

Video links:

https://www.youtube.com/watch?v=Vm3z2sbCCA4&feature=youtu.be

https://www.youtube.com/watch?v=wX_gi95h5oY&feature=youtu.be

4.2 . An female in estrus drumming her feet against a focal tree with accumulated stones.

Description:

21 November 2019 at 17h54: an female in estrus was recorded to drum her feet against a focal tree, accompanied by typical swaying and pant-hoot vocalization.

Video link:

https://youtu.be/_TDiXY_g7-o

Recorded by Sem van Loon, Foundation Chimbo

4.3. Females climbing a focal tree.

Description:

4 July 2019 at 6h57: a young female is drumming hands and feet rhythmically on a focal tree, while she is climbing upwards, out of camera view. She also smells the bark of the tree. She is followed by an adult male chimpanzee. The adult male sits for some seconds (23s) on a stone near the tree, sways back and forth, then drums his feet against the buttress root of the tree, accompanied with pant-hoot vocalization, while climbing upwards. Both chimpanzees leave camera view but soft chimpanzee vocals can still be heard. (Video 1).

2 July 2015 at 11h32: a young female (possibly with a disabled hand) was recorded to climb into a focal tree just before a party of chimpanzees of at least 9 adults passed by, after which she climbs down from the tree to inspect the camera and especially the accumulated stones and the trunk of the tree, before climbing back into the tree (Video 2).

Video links:

1) https://youtu.be/t9KkQhznoKY

2)

https://www.youtube.com/watch?v=5SHbF1EdqvM&feature=youtu.be

Box 4: Discussion of particular observations of female adult chimpanzees at accumulative stone throwing sites.

Discussion

Chimpanzee female accumulative stone throwing is particularly poorly understood, and therefore, we advocate paying attention to female observations and not discarding them only because it may not be of interest for the current, proposed hypothesis.

Sex-differences in wild chimpanzee behavior emerges during infancy (Lonsdorf et al. 2014) and have already been recognized for social interactions, foraging behavior, ranging patterns and tool-use (e.g., Gruber et al. 2010; Murray et al. 2007; Wrangham and Smuts 1980). Better quality cameras positioned in different angles around the trees, together with field visits, might help to distinguish more accurately males from females when performing analyses.

Observations of chimpanzee accumulative stone throwing by females have until now been exclusive to the Boé, reporting only two different individuals (Buys 2016; Kühl et al. 2016). Out of a record of 235 accumulative stone throwing events in Boé in 2018-2020, Van Loon (2020, unpublished data) did not observe any female performing accumulative stone throwing, while she observed three times an adult female drumming her feet on a focal tree (in comparison to 84 male drumming events). This is in line with previous studies on (buttress) drumming (e.g., van Lawick-Goodal 1986) and tool-use for sound production (Dufour et al. 2017): males are much more involved than females. Many studies on buttress drumming investigate therefore mainly male behavior (Arcadi 1998, 2004; Babiszewska et al. 2015; Dufour et al. 2017). As such, particular cases on female accumulative stone throwing are worth mentioning.

The elderly female in the first observation clearly shows the same particular non-aggressive display related traits that have been observed in male chimpanzees when stone throwing: e.g., swaying, piloerection, bipedal standing and pant-hoot vocalization. She might have been an alpha-female, but we lack details on the social-hierarchical context. Other hypotheses are therefore not excluded.

We added two descriptions of female chimpanzees climbing a focal tree, one while drumming and possibly attracting a male chimpanzee to follow her, while the other one climbs another focal tree just before, remaining there until a party of 9 chimpanzees with mainly male adults has passed. We cannot be sure whether it is just a haphazard coincidence that the tree they climb is a focal tree (as chimpanzees often climb trees); but at the moment they come into camera view they walk resolutely to the tree and climb into it. The first female chimpanzee is drumming rhythmically but softly with her hand and feet while climbing the tree. The second chimpanzee is inspecting the pile of stones that are accumulated in another focal tree's cavity after which she is climbing the tree as well.

We do not know the extent to which the function of accumulative stone throwing or accumulative stone throwing sites and focal trees alters depending on gender. Sexual differences and contexts might also differ among groups. Lehman and Boesh (2008), indicated that female associations are much stronger within male pilopatric systems in West-Africa (investigated for Cote d'Ivoire) than in East-African regions. (Guinea Bissau being the outermost region of Western-chimpanzee distribution).

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