Unusual feeding behavior in wild great apes, a window to understand origins of self-medication in humans: Role of sociality and physiology on learning process

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ABSTRACT

Certain toxic plants are beneficial for health if small amounts are ingested infrequently and in a specific context of illness. Among our closest living relatives, chimpanzees are found to consume plants with pharmacological properties. Providing insight on the origins of human self-medication, this study investigates the role social systems and physiology (namely gut specialization) play on learning mechanisms involved in the consumption of unusual and potentially bioactive foods by two great ape species. We collected data from a community of 41–44 wild chimpanzees in Uganda (11 months, 2008), and a group of 11–13 wild western gorillas in Central African Republic (10 months, 2008–2009). During feeding, we recorded food consumed, its availability, and social interactions (including observers watching conspecifics and the observers' subsequent activity). Unusual food consumption in chimpanzees was twice higher than in gorillas. Additionally chimpanzees relied more on social information with vertical knowledge transmission on unusual foods by continually acquiring information during their life through mostly observing the fittest (pre-senescent) adults. In contrast, in gorillas observational learning primarily occurred between related immatures, showing instead the importance of horizontal knowledge transmission. As chimpanzees' guts are physiologically less specialized than gorillas (more capable of detoxifying harmful compounds), unusual-food consumption may be more risky for chimpanzees and linked to reasons other than nutrition (like self-medication). Our results show that differences in sociality and physiology between the two species may influence mechanisms that discriminate between plants for nutrition and plants with potential therapeutic dietary components. We conclude that self-medication may have appeared in our ancestors in association with high social tolerance and lack of herbivorous gut specialization.

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1. Introduction

A number of plants consumed as food are recognized as having pharmacological properties alongside their nutritional value and are purposely ingested as medicine in certain traditional human societies. Additionally, a large number of drugs used in modern medicine are, or have been, obtained from plants, or were discovered from their traditional use: coca from Incas, quinquina from Amazonians, antitumoral vinblastine and vincristine from *Catharanthus roseus* (Madagascar Periwinkle) from Malagasies [1,2]. To understand the evolution of human medicine and diet, a hypothesis based on the positive role of dietary plant secondary compounds and a synergistic balance between the nutritional and pharmacological properties of foods have been proposed [3]. How humans

came to use plants for medicine is still unknown. Our closest relatives, the great apes, are naturally susceptible to many diseases including parasites that afflict humans and probably our hominid ancestors [4,5]. Thus, observation of great apes can provide a powerful tool in understanding both human evolutionary and cultural aspects of the origins of plant selection for food and medicinal properties.

Chimpanzees are known to consume some plants with low nutritional value and/or high bioactive compounds possibly to maintain and improve their health suggesting a self-medicating role [6–11]. Indeed, phytochemical analysis of such plants has revealed the presence of bioactive compounds effective against systemic and intestinal parasites, and antitumor properties [12–18]. Additionally, the simultaneous ingestion of soil and bioactive leaves of *Trichilia rubescens* by chimpanzees was shown to increase antimalarial bioactivity, suggesting the existence of complex feeding behaviors [19]. Why great apes should search for bioactive plants and how they learn to consume them has been little investigated. Additionally, it is not yet clear what is the role of genetic

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predisposition and what of individual or social learning on the appearance of those behaviors and the possible transmission between generations.

In general, primates react towards novel foods with caution [20,21]. This neophobia may have evolved in parallel, but independently of the unpalatable taste of certain plant parts (e.g. bitter taste, astringency) indicating the presence of toxic secondary compounds, considered as a defense of plants against herbivores, although linked to the intensity of gustatory perceptions [22–24].

Nevertheless, through the consumption of a large diversity of plants together with a high tolerance to toxic compounds (e.g. condensed tannins, phenols, alkaloids), great apes ingest alongside nutrients, numerous chemical constituents abundant in vegetative plant parts on a daily basis [25–29].

Similar to our modern drugs, if certain secondary substances are ingested in small quantities (below the toxic threshold) they can have beneficial effects towards maintaining health or disease recovery; under these circumstances the medicinal benefits may be greater than the plant's nutritional value [9,30]. The balance between beneficial (health gains, nutrition) and detrimental effects (toxicity) also depend on the animal's body size and its physiological ability to detoxify harmful compounds. Thus, differences can be found both between species (ruminant-like stomachs/enlarged hindgut and fermentation processes) and within species (e.g. immature individuals vs. adults) [22,31,32]. Varying physical and physiological tolerances towards toxicity may also lead to different levels of neophobia [33,34]. In general, young primates including humans are less neophobic than adults [33,35,36]. However, when human children become more mobile and independent, food neophobia increases rapidly and then decreases during puberty [37]. As sub-adults often disperse during puberty in human and non-human primates, lower neophobia may be adaptive to deal with changes in food availability in new areas. Being close to adult body size, sub-adults may equally be more tolerant of higher adult doses of toxic plant compounds [38,39].

Given the discussed advantages and disadvantages of neophobia, how can young animals overcome this adaptive reluctance to novelty whilst acquiring the adult diet? To avoid the risks of toxicity associated with individual exploration during the learning process, immature animals require social information through co-foraging. In general, a higher reliance on social learning is predictable the higher the level of sociality of a taxon (primates: [40–43], other mammals: [44,45]). Observational learning and diet synchronization are probably the main mechanisms responsible for transmission of food preferences between generations in highly social animals (primates: [41,46–48], other mammals: [44,49], fish: [50]). Older and more successful individuals (e.g. high ranking) are expected to be the best model to copy, and are mainly responsible for generating and transmitting food traditions [51,52]. Besides observation and diet synchronization, food transfer from mother to infant has been suggested to be an important means to transmit nutrient and food information in primates, particularly in great apes who highly depend on extractive foraging techniques which are difficult to learn independently [53–55]. Active teaching of infants by mothers seems to be a unique trait of human beings (great apes: [56,57], humans: [52]), but difficult or dangerous skills may require some teaching in some animal species (primates: [58,59], other mammals: [60]).

Both chimpanzees (*Pan troglodytes*) and western gorillas (*Gorilla gorilla*) are highly frugivorous showing significant dietary flexibility in response to the large seasonal and inter-annual changes in fruit availability in tropical forests [61–65]. Due to the different levels of complexity of their social systems — fission–fusion society in chimpanzees and one-male harems in western gorillas — chimpanzees and western gorillas probably face different levels of within-group feeding competition [66,67]. In contrast to western gorillas, chimpanzees remain mainly frugivorous throughout the year, even when sharing the same habitat [68,69]. On the other hand, the longer gut retention time and enlarged hindgut with more cellulose-digesting ciliates [31,70] allow gorillas to digest foods high in fiber and/or toxins, and to shift to a herbivorous diet when fruit is scarce [27,63]. Additionally, while chimpanzees and orangutans are well known for their ability to develop foraging tools and rely on social learning for transmitting these behaviors within their social groups, gorillas are comparatively poorly studied (chimpanzees: [35,57,58], orangutans: [41,71]). Therefore, it is not clear if gorillas develop such "traditions": a recent study suggests they do ([72] but see also [73]) however until very recently they have been thought to develop feeding techniques solely by a mixture of genetic predisposition and individual learning [74]. Are these differences also found in relation to the consumption of potentially toxic plants that may also, in limited amounts, be beneficial for health? Or in this case do they share a similar process of dietary knowledge acquisition?

With the ultimate goal of understanding mechanisms of great ape knowledge acquisition of bioactive plants, in this study we focus on consumption of "unusual" foods, i.e. food that is rarely fed upon, with low energetic/nutritional content and/or known bioactivity, by chimpanzees and western gorillas. If an unusual food is toxic and consumed for other reasons than nutrition (such as to treat a disease), we predict, if the availability of unusual foods is equivalent in both their habitats: 1) a higher frequency of unusual food consumption in chimpanzees than in western gorillas, since western gorillas are more herbivorous and already likely to ingest a larger quantity/diversity of secondary compounds daily; 2) regardless of species a higher frequency of unusual food consumption in larger size individuals given their higher tolerance towards toxins with respect to smaller individuals. If consumption of unusual food is socially learnt we expect 3) a higher frequency of direct interactions (e.g. food transfers, inter-individual observations, inhibition behaviors by adults towards immature individuals ingesting non-food items) among the highly social chimpanzees than in western gorillas, and 4) that immature individuals more frequently watch older (experienced) individuals, who may play a role as demonstrators.

Understanding the role played by sociality in diet acquisition helps us to assess the potential response of endangered primates to habitat change, which may affect the availability of plants both usually and rarely consumed, and which may be important for both nutrition and health maintenance.

2. Methods

2.1. Study area and study animals

Chimpanzee data were collected during 11 months in 2008 on a habituated community ranging in 32 km^2 at Kanyawara, in the north-west of Kibale National Park, Uganda. During the study period the community composition ranged between 41 and 44 individuals due to three births and three migrations of sub-adult females (nineteen adults, seven to ten sub-adults, eleven juveniles, two to four infants; age-classes following [75]). Chimpanzee data on community composition were recorded every 15 min from January to August 2008 and from October to December 2008 by S.K. and field assistants ($N_{Days} = 237$, $N_{Hours} = 2000$). During this period the mean party size (sub-groups related to the fission–fusion social system) per day was 16 individuals (range: 1–34). Western gorilla data were collected at Bai-Hokou by S.M. from April to July 2008 and from November 2008 to March 2009. The study group is a habituated group — Group Makumba — ranging during this study in 13 km^2 in the Dzanga-Ndoki National Park, Central African Republic. During the study period the group composition ranged between 11 and 13 individuals (one silverback, three adult females, one blackback, zero to two subadult females, three juveniles and three infants; following [38]) due to emigrations by the two sub-adult females. Focal animal sampling [76] of all age/sex classes was carried out during half days and occasionally full days of observations ($N_{Days} = 214$, $N_{Hours} = 818$).

Further information on both study sites are described elsewhere [16,62].

2.2. Data collection

For each study site a list of unusual and bioactive foods (UBF), defined as rarely eaten food items but consumed by more than one individual and/or having biological properties, was established a priori on the base of a) low consumption frequency from long-term data (<1% of feeding time of all food item consumed during a year-time), b) clear low energetic value (e.g. dry leaves, soil, decaying wood), c) previous results of bioassays [8,9,15,16,77], d) phytochemical literature and/or traditional uses in local medicine (Table 1). When an individual consumed an unusual food, the plant species, the type of UBF item ingested (young/mature/dry leaves, petioles, pith, flowers, ripe/unripe fruits, seeds, trunk bark, root bark, decaying wood and soil), the quantity ingested, and the duration the item took to be consumed were recorded. Every "new" UBF item consumed during the study period was added to the lists (Table 1). Food consumption was defined when an individual kept the food item in the mouth for at least 30 s which did not involve playing. In the forest, experienced field assistants and knowledgeable Ba'Aka pygmy trackers helped to identify plants consumed by the study subjects. Herbaria of unknown plants eaten by chimpanzees were identified at the Makerere University Biological Field Station, Uganda and the National Museum of Natural History, France.

To exclude infrequent ingestion of UBF items that was related to low availability of the food, an abundance score of the UBF item (none, rare, common, and abundant) within 20 m around the consumer was noted for every UBF consumed. Additional information on spatial availability of UBF plant species in the study areas were obtained for 17 trees (diameter at the breast height: DBH>10 cm) and seven ground layer species (herbaceous, shrubs and saplings/poles: DBH<10 cm) out of the total 36 UBF species consumed by chimpanzees from vegetation densities determined in Kanyawara by other authors [135–137]. For gorillas, densities of nine trees and six ground layer species out of the 23 UBF plant species were obtained from a previous study based on 59 transects of 340 m placed in the home range of the study group [138,139].

In order to estimate the probability that UBF consumers were observed by conspecifics and make a comparison between the two ape species, all individuals present within 15 m from consumers were recorded at each UBF consumption. The food species and food type ingested by these individuals were also noted, their orientation towards the consumer (facing the consumer or not), and the visibility between the individual and the consumer (0: no visibility between the two individuals due to obstacles — shrubs, trees; 1: partial visibility only due to the presence of vegetation or other individuals; 2: clear visibility). To test the hypothesis that social context plays a role in overcoming neophobia and consequently selecting bioactive food in the correct quantity (to avoid being poisoned) and in the right context (i.e. when sick), all occurrences of social interactions among individuals (aggressive, inhibiting and affiliative behaviors, vocalizations, food transfers, watching of food consumers), and the distance between the interacting individuals were recorded whilst feeding on both usual and unusual food. The activity of individuals after they begged or watched a consumer feeding was recorded (fed on the same food, fed on another food, stealing food, and other activities).

Health monitoring of the study subjects was carried out throughout the study period; however, since these results go beyond the goals of the present study, they will be presented in another manuscript [140].

2.3. Definitions

Inhibition was defined in relation to feeding context and distinguished from aggressive behavior when involuntary transfer of a defendable food occurred from the possessor to another individual and no aggressive vocalizations or reactions from either individual occurred (e.g. stealing without resistance, mother removing plants from the infant). Food transfer was defined as any voluntary transfer of the item from one food-motivated individual to another individual, initiated either by the giver or the receiver

[42,54]. Watching was defined as continuous observation by an individual (the observer) of another (the consumer or demonstrator). In the data analysis, only watching events that occurred after the following criteria were included: a) observers were in a positive orientation towards the consumer, b) the visibility was at least of category 1 (see Methods), c) the maximum distance between observer–consumer was 15 or 10 m respectively for chimpanzees and gorillas (visibility being more limited in the gorilla study site), d) the minimum duration of watching bouts was 5 s. Begging was distinguished from watching when soliciting for food was involved (extending hand, begging grimace, trying to remove food from the consumer, mouthing and/or specific vocalizations towards the food possessor) [42]. Given the absence of typical easily-interpretable facial expressions and extending hand behaviors in the western gorillas' repertoire as described in chimpanzees ([67], Masi and Gustafsson pers. observ.), watching and begging were often difficult to distinguish for gorillas. To avoid subjectivity we considered watching as all observing behaviors that did not fit into our begging definition and did not involved food transfer.

2.4. Calculations of frequencies and class subdivisions

Frequency of UBF consumption per day (12 daylight hours) per individual present was calculated as the daily average number of UBF consumption events for each day of the study period corrected for the different group sizes (for chimpanzees, the daily mean party size and for gorillas, the maximum size of the group) and the number of hours of focal follows per day (i.e. full days and half days of focal follows).

When investigating the possible influence of body size and physiology on the consumption of UBFs, the study animals were pooled in two broader classes: 1) immature size individuals (including juveniles and infants: $N_{Chimpanzees} = 12–15$; $N_{Gorillas} = 6$) and 2) mature size individuals (adults and sub-adults: $N_{Chimpanzees} = 26–29$; $N_{Gorillas} = 4–6$), based on the fact that body size of sub-adult chimpanzees and western gorillas is similar to adult size [38,39]. Thus, differences were investigated based on the assumption that individuals within each class have roughly the same tolerance to toxic compounds. Even though in gorillas, silverbacks are approximately double the size of adult females they were pooled together into the mature class since no statistical differences were found when their data were analyzed separately. Both classes were equally observed during the study periods (chimpanzees: $N_{Days\ Immatures} = 68$, $N_{Days\ Matures} = 72$; western gorillas: $N_{Days\ Immatures} = 101$; $N_{Days\ Matures} = 122$).

Due to the low number of individuals in each age category for the gorilla group, to compare and investigate the effect of age on social learning we used two broad age classes modifying the classes defined above considering that: 1) overall infants, juveniles and sub-adults are expected to have a lower degree of neophobia with respect to adults, and 2) in chimpanzees males do not disperse at adulthood, and in western gorillas males emigrate at least 5 years later than females [38,75]. Therefore, we pooled sub-adult females with the immature class (Immature + Sub-adult Females), while the mature class (Mature) consisted of adults and sub-adult males only. Rates of begging and watching conspecifics were calculated per each of these age classes dividing the number of events by the total time spent feeding on usual or unusual food by chimpanzees and gorillas respectively. Begging and watching rates during usual (normal) feeding sessions were calculated for chimpanzees from 177 feeding sessions of 11 min each ($N_{food\ items} = 44$, $N_{species} = 41$) recorded during the study period, and for gorillas from daily focal following using for total feeding time the daily average time spent feeding from a previous study carried out by S.M. on the same study group [62].

2.5. Phytochemistry and ethnobotanical survey

The dried and powdered plant material was extracted and bioactive properties of plants (Table 1) were tested following the same methods as described in a previous publication [9].

Table 1
Potential pharmacological properties and human use in traditional medicine of unusual and bioactive plants (UBF) of chimpanzees (A) and western gorillas (B).

A) CHIMPANZEES

Species	Family	Part	# UBF consumptions recorded	Uses in traditional medicine	Biological activities — part: (molecules) chemical or mechanical activity
Aneilema aequinoctiale Kunth	Commelinaceae	Leaves	1		Rough leaves: deworming agent [77]
Antiaris toxicaria Lesch.	Moraceae	Leaves	36	Latex: dart poison [78]	Latex: (cardiotonic cardenolides) anti-tumoral [78]
Bosqueia phoberos Baill.	Moraceae	Leaves	5		Bark: bacteriostatic [93]
Chaetacme aristata Planch.	Ulmaceae	Bark	4	Leaves: anti-tuberculosis [79]; bark: hemorrhoids [80]	Bark: bacteriostatic [9]
Cordia abyssinica R.Br.	Boraginaceae	Pith	1	Bark stems: stimulant, anti-hemorrhage [81], cold, influenza, leprosis [82]; leaves/pith: anti-tuberculosis [79]	Leave/pith: anti-malarial, anti-tubercolusis, bactericidal[a]
Diospyros abyssinica (Hiern) F. White	Ebenaceae	Leaves	1	Leaves/seeds: wound, foot fungal infection [83]	Bark: (bisnaphtoquinones) anti-malarial, anti-leishmania, anti-helmintic and bactericidal [9]
Ficus capensis Thunb.	Moraceae	Leaves	1	Fruits: leprosis [84], laxative, abortifacient, aphrodisiac, pain [85]	Bark/leaves: (alkaloids, balsams, taninins, carbohydrates, resins, flavonoids, sterols and terpenes) anti-bacterial [94]
Ficus exasperata Hort.Kew. ex Miq.	Moraceae	Leaves	4	Leaves: edema, leprous ulcer [84], dermatosis, abscess [81]	Leaves: bacteriostatic [93], anti-ulcerogenic, delayed intestinal transit, incread the pH, decrease both volume and acidity of gastric secretion in rats [95]; rough Leaves: deworming agent [77]
Ficus exasperata Hort.Kew. ex Miq.	Moraceae	Unripe fruits	1		
Ficus natalensis Krauss ex Engl.	Moraceae	Bark	1	Whole plant: veneral disease; bark: diarrhea, influenza, galactogenic [10]	Leaves: bacteriostatic (*S. aureus* and *E. coli*)[a]
Ficus stipulifera Hutch.	Moraceae	Leaves	1		Leaves: bactericidal (*S. aureus*), anti-malarial[a]
Ficus urceolaris Welw. ex Hiern/*Ficus asperifolia* Miq.	Moraceae	Leaves	14	Leaves: fever, sterility [83]	Rough leaves: deworming agent [77]
Ficus urceolaris Welw. ex Hiern/*Ficus asperifolia* Miq.	Moraceae	Unripe fruits	16		
Illigera pentaphylla Welw.	Hernandiaceae	Leaves	4	Leaves juice: dyspnea [83]	Leaves: bactericidal (*S. Aureus*), anti-malarial[a]
Jasminum abyssinicum Hoscht. Ex DC.	Oleaceae	Leaves	22	Leaves: anthelminthic [86]	
Lepisanthes senegalensis Poiret	Sapindaceae	Leaves	1		Leaves: anti-malarial[a]
Mimusops bagshawei S. Moore	Sapotaceae	Leaves	3		Leaves: anti-malarial [9]
Monodora myristica Blanco	Annonaceae	Leaves	2	Seeds: anti-helmintic, gastric disease [78], wounds, anti-emetic, tonic, headaches and rhinopharyngitis [83]	Bark: anti-helmintic [9]; leaves: anti-malarial[a]
Myrianthus arboreus P. Beauv.	Moraceae	Leaves	1	Leaves: analgesic for teeth, throat pain [83], dysentery and urethral discharge [87]	Leaves: anti-malarial[a]
Neoboutonia macrocalyx Pax	Euphorbiaceae	Dead wood	12	Bark/leaves: stomach ache, malaria, fever [82,85], dysentery [88], abortion (Kasenene pers. comm.), psychosis, witchcraft [89]	Dead wood/bark root: anti-malarial[a]
Neoboutonia macrocalyx Pax	Euphorbiaceae	Bark root	3		
Neoboutonia macrocalyx Pax	Euphorbiaceae	Dead wood/leaves	1		
Olea welwitschii Knobl.	Oleaceae	Leaves	2	Bark: gonorrhea [9], cough [90]	Not significant anti-malarial and cytotoxicity [93]
Parinari excelsa Sabine	Chrysobalanaceae	Leaves	1	Bark/leaves: fortifying pregnant femal, anemia, rheumatism, pains [84], dental and mouth pain, sexual incapacity, aphrodisiac [79]	Bark: anti-malarial, cytotoxic[a]
Phytolacca dodecandra L'Hér.	Phytolaccaceae	Unripe fruits	7	Fruit: bilharziosis [90]	Fruits: (triterpene saponins) toxicity, molluscicidal, anti-viral, anti-bacterial, spermicidal, anti-fertilizing activity [87,96,97]
Pseudospondias microcarpa Engl.	Anacardiaceae	Leaves	9	Bark/leaves: cough, anthelmintic [78], fever, intoxication, weakness, diarrhea, gonorrhea [83]	
	Rubiaceae	Root	1		Pith: anti-malarial[a]

Table 1 (continued)

A) CHIMPANZEES

Species	Family	Part	# UBF consumptions recorded	Uses in traditional medicine	Biological activities — part: (molecules) chemical or mechanical activity
Psychotria mahonii C.H. Wright					
Pterygota mildbraedii Engl.	Sterculiaceae	Leaves	8		Leaves: bacteriostatic [93]; bark: anti-malarial[a]
Pterygota mildbraedii Engl.	Sterculiaceae	Bark from dead tree	1		
Rothmannia urcelliformis (Hiern) Bullock	Rubiaceae	Leaves	1		Not significant anti-malarial and cytotoxicity[a]
Rubia cordifolia Hochst. ex A.Rich.	Rubiaceae	Leaves	5	Leaves/roots: eye infection, tape worm [89], pleurisy, chest inflammation, relieve pain [9]	Rough leaves: deworming agent [77]
Solanecio manii (Hoock. f.) C. Jeffrey/*Crassocephalum mannii* (Hook. f.) Milne-Redh.	Asteraceae	Pith	2	Leaves/stem: wounds, purgative, edema, skin lesion, absciss, disentery, cardiac pain, delivery baby, urinary disease, malaria, fever, asthma [85]	Not significant anti-malarial and cytotoxicity[a]
Stephania abyssinica (Dill. & A. Rich.) Walp.	Menispermaceae	Root	1	Leaves/stem: contusion, dysentery, fracture, headache, sterility, cystitis, anemia, rachitis, stomach pains, colitis, diabetes[85]	
Tabernaemontana (*Cronopharyngia*)	Apocynaceae	Fruit	1	Bark/roots: aids in baby delivery, pneumonia, chest problems [91]	
Teclea nobilis Del.	Rutaceae	Leaves	1	Leaves/bark: malaria, anemia, rachitis [92]	Bark: anti-malarial[a]
Trichilia rubescens Oliv.	Meliaceae	Leaves	171	Bark/leaves: rectal ulcer, dysentery, enema as purgative, soporific, bruises, dysentery [9] gonnorrhea [83]; Seeds: itching, rheumatism, enema as purgative [9]	Leaves: (limonoids) anti-malarial, anti-helmintic, bactericidal [15]
Unidentified fern	Unknown	"Leaves"	1	Unknown	
Unknown 1	Unknown	Leaves	1	Unknown	
Unknown 2	Unknown	Dry wood	1	Unknown	
Unknown 3	Unknown	Leaves	1	Unknown	
Unknown 4	Unknown	Fruit	1	Unknown	

B) WESTERN GORILLAS

Species	Family	Ba'Aka name	Part	# UBF consumptions recorded	Uses in traditional medicine	Biological activities — part: (molecules) chemical or mechanical activity
Anonidium mannii (Oliv.) Engl. & Diels	Annonaceae	Mobei	Seeds in elephant feces	2	Bark: sore feet[a,b], spider bite, bronchitis, dysentery, women sterility caused by poison, gastroenteritis [98]	Stem/bark: (prenylated bisindole alkaloids) [108]
Anonidium mannii (Oliv.) Engl. & Diels	Annonaceae	Mobei	Rotten fruit	1		
Anonidium mannii (Oliv.) Engl. & Diels	Annonaceae	Mobei	Rotten seeds	21		
Barteria fistulosa Mast.	Passifloraceae	Ngomangoma	Leaves	4	Root: obstetric use (help baby deliver) [98]	Bark/leaves: (flavones, saponines, acide cyanhydrique) anti-inflammatory, analgesic [109]
Camptostylus mannii (Oliv.) Gilg	Flacourtiaceae	Moangwale	Fruit	1	None[a,b][98]	Roots: (flavonoid) [110]
Detarium macrocarpum Harms	Caesalpiniaceae	Eboto	Growing Bark after elephant stripped it	2	Bark: diuretic, anti-inflammatory, anti-parasitic, dysentery and syphilis [80,96,99]	Seeds: (steroidal saponins, flavonoids) anti-microbial [111], (terpenoids, flavans) anti-HIV [112]; bark/bark grown after elephant strip it: anti-*Candida albicans*[a]
Erythrophleum suaveolens (Guill. and Perr.) Brenan	Caesalpiniaceae	Ngbanda	Old fruit	2	Bark: killing or suicide poison, inducing vomit, against fainting, crisis, abscess with fever, wound [98]	Bark: (procyanidins) anti-inflammatory, analgesic [113], (saponins, tannins, steroids, alkaloid) anti-bacterial [114]
Gambeya lacourtiana (DeWild.) Aubrev. & Pellegr.	Sapotaceae	Bambu	Seeds in elephant feces	2	Bark: healed wound and disinfect them[a,b][98], plant galactologue [98]; Fruit: vaginal infections, rheumatism, uterine hemorrhage [100]	Stem/bark/seeds (*Gambeya* spp.): (pentacyclic triterpenoid, saponins, steroid glycosides) [115,116]

Table 1 (continued)

B) WESTERN GORILLAS						
Species	Family	Ba'Aka name	Part	# UBF consumptions recorded	Uses in traditional medicine	Biological activities — part: (molecules) chemical or mechanical activity
Hexalobus crispiflorus A. Rich.	Annonaceae	Pota	Seeds in elephant feces	1	Leaf/seeds: malaria [101]	Bark/leaves/seeds: (terpenoids) anti-malarial [117], (diprenyl-substituted indoles) anti-fungal [118]
Marantochloa congensis (K. Schum.) Leonard and Mullend.	Marantaceae	Mbili	Leaves	1	Roots: purgative [100]	
Milicia excelsa (Welw.) C.C. Berg	Moraceae	Mobangi	Petioles of dead dry leaves	11	Bark: sedative [102]	Petioles: anti-leishmania[a]
Milicia excelsa (Welw.) C.C. Berg	Moraceae	Mobangi	Dead dry leaves/ petioles	4		
Palisota ambigua (P. Beauv.) C. B. Clarke	Commelinaceae	Doto	Leaves	10	Stem juice: irritating substance in arrow poison, alleviation of pain in snake bite[a,b]	Leaves: (ecdysteroids) [119], inducing hyperthermia and prolonged sleep in mice [120]
Palisota ambigua (P. Beauv.) C. B. Clarke	Commelinaceae	Doto	Flowers	1		
Platycerium sp.	Polypodiaceae	Uya	Leaves	1	Whole plant: hypertension, cardiac palpitations [103]	Leaves (*Platycerium* spp): (flavonoid) anti-oxidant, anti-inflammatory [121], anti-bacterial [122]
Porterandia sp. ?	Rubiaceae	Ngobo	Leaves	1	Leaves: aphrodisiac, eczema, diarrhea, local pain relief [100,102]	Leaves: anti-leishmania[a]
Pyrrosia sp.	Polypodiaceae	Ita ti Uya	Leaves	1	Whole plant: diuretic, disorders of the urinary tract [104]	Leaves: (flavonoid) anti-viral against herpes simplex [123,124]
Selaginella sp.	Selaginellaceae	Ita ti Benjem	Leaves/ vine stem	7	Leaves: anti-hemorrhagic, snake bite [105]	Leaves (*Selaginella* spp.): (biflavonoids) antiviral [125], cytotoxic [126,127]
Strophanthus tholloni Franch.	Apocynaceae	Ndemele - Monbango - Melangena	Bark/ leaves	2	Bark: one of the major ingredients for arrow poison[a]	Root/bark/leaves (*Strophanthus* sp.): (cardenolide glycosides) anti-tumoral [128]; Leaves (*Strophanthus* sp.): (alkaloids, flavonoids, saponins, cardiac and cyanogenic glycosides) hypoglycemic effects [129]
Strophanthus tholloni Franch.	Apocynaceae	Ndemele - Monbango - Melangena	Leaves	1		
Terminalia superba Engl. & Diels	Combretaceae	Ngolu	Bark	1	Bark: hernia pain [98], diabetes [106]; Leaves: malaria [107]	Bark: (gallic acid, methyl gallate, methanol and methylene chloride) anti-diabetic [106,130]; Leaves: anti-malarial [106]
Terminalia superba Engl. & Diels	Combretaceae	Ngolu	Dead dry leaves	13		
Thomandersia hensii De Wild. & T. Durand	Acanthaceae	Inguka	Leaves	1	Leaves: anti-helmintic[a], rheumatisms, abscess/ wound from chameleon or toxic ant, pruritus, inducing vomit after sneake bite [98]; leaves/roots: coughs, fevers, asthma, dysentery, fatigue, vaginal infection [100]	Bark (*Tomadersia* sp.): anti-malarial [131]; Leaves: (indolinone alkaloids) [132]
Thomandersia hensii De Wild. & T. Durand	Acanthaceae	Inguka	Flowers	1		
Treculia africana Deecne.	Moraceae	Wusa	Hard inner part of the Fruit	1	Roots: anti-miscarrige [98], male medicine[a]; fruit/ leaves: chronic coughs, skin infections, anti-helmintic [100,102]	Fruit: (hydrophilic polysaccharide) simulation of gastric and intestinal fluid [133], (polyphenols) teratogenicity [134]
Trichilia sp.	Meliaceae	Maimbo	Bark	5	Bark/leaves: rectal ulcer, dysentery, enema as purgative, soporific, bruises, dysentery [9] gonnorhea [83]; Seeds: itching, rheumatism, enema as purgative [9]	Leaves (*Trichilia rubescens*): (limonoids) anti-malarial, anti-helmintic, bactericidal [15], anti-leishmania[a]

Table 1 (continued)

B) WESTERN GORILLAS						
Species	Family	Ba'Aka name	Part	# UBF consumptions recorded	Uses in traditional medicine	Biological activities — part: (molecules) chemical or mechanical activity
Unknown 1	Fabaceae	Elembonjoku - Dietenge	Fruit	1	None[a]	
Unknown 2	Unknown	Mbongombongo	Leaves	1	Unknown	
Unknown 3	Rubiaceae	Mondamandama simple	Leaves	4	None[a]	
Unknown 4	Rubiaceae	Mondamandama ti poil	Leaves	7	None[a]	
Unknown 5	Rubiaceae	Mondamandama rouge	Leaves	1	None[a]	

[a] This study (percentage of inhibition at 10 µg/ml).
[b] M. Fay, Ethnozoological notes on the knowledge of one male Ba'Aka by large forest mammals and man of forest plants, unpublished notes.

Ethnobotanical survey among Ba'Aka pygmy trackers was conducted by S.M. during the study period for the plants consumed by gorillas. Purpose and part used in traditional medicine were recorded.

2.6. Statistical methods

To investigate differences in the frequency of UBFs consumed between the two ape species we used Mann–Whitney U tests, each day representing an independent data point. The same test was also used to investigate differences within each species in watching frequency between the age classes, and to analyze the influence of age class on the probability of being an observer or a demonstrator (and thus being watched by others), using either each individual or watching event as an independent data point. Before carrying out these tests, we first divided the number of watching events per individual by a) the number of days a chimpanzee was observed in the party, or b) the number of hours of focal follows for a gorilla. In contrast to the gorillas, the age of individual chimpanzees was known precisely thus we could display a graphical representation of the age of UBF consumers against the number of UBFs consumption events with observers. The chimpanzee data seemed to fit a quadratic relationship (individuals who did not consume and did not observe were omitted). Thus, to further investigate the influence of age of consumers on the probability of being demonstrators we carried out a linear regression with quadratic effect using as predictor variables the log-transformed age of consumers to match the normality requirements (Shapiro–Wilk Normality Test: $N = 17$, $W = 0.98$, $P = 0.926$). To investigate differences in watching frequency between the consumption of UBF and usual food within the same ape species we used Wilcoxon tests based on averages per feeding session (UBF or usual food) and using as independent data points the age/sex classes for each species [38,75].

3. Results

Hypothesis 1. Given that western gorillas have a more herbivorous diet and a greater microbial ability to detoxify secondary compounds, if UBF availability is similar, frequency of UBF consumption is expected to be lower than in chimpanzees.

During the whole study period, daily frequency of consumption of UBFs (F_{UBFs} for plants and soil) was twice as high in chimpanzees than in gorillas (F_{UBFs}: 0.27 vs. 0.14; controlling for group size and observation time per day: Mann–Whitney U test, $N_{Chimpanzees} = 232$, $N_{Gorillas} = 214$, $z = -8.45$, $P \ll 0.001$; UBF plants without soil: $N_{Chimpanzees} = 221$, $N_{Gorillas} = 212$, $z = -7.21$, $P \ll 0.001$), for a total time spent feeding on unusual items of 2000 min and 750 min for chimpanzees and gorillas respectively. Comparative results on consumption of UBFs are shown in Fig. 1 and availability of UBF species in the two species homeranges are summarized in Table 2. Among the identified UBF plant species, 34% of UBF species for chimpanzees ($N = 35$) and 19% for gorillas ($N = 21$) were also part of their usual yearly diet but for different plant parts (Table 2). After the first consumer, items of the same UBF species, besides the ones consumed, were available in the majority of chimpanzee (76%, $N = 315$) and gorilla cases of consumption of UBFs (96%, $N = 29$).
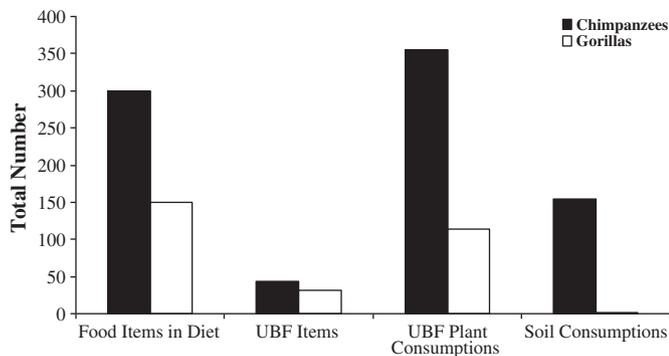

Fig. 1. Comparative summary of diet repertoire from the long term data (*Food Items in Diet* — includes UBF plant items, soil and animal matter) and the results of consumption of UBFs in chimpanzees and western gorillas during the study periods. The number of *UBF Items* includes soil and plants.

Table 2
Comparative summary of results of UBF species availability in chimpanzees and western gorillas' home-ranges.

Species	N_{Tot} of UBF plant species	% of UBF common trees[a]	% UBF ground layers with comparable density of usual food[b]
Pan troglodytes	36	82 ($N = 11$)	100 ($N = 7$)
Gorilla gorilla	24	33 ($N = 9$)	67 ($N = 6$)

[a] *% of UBF Common Trees*: percentage of UBF tree species consumed by the study animals that are common (at least 1.00 individual/ha) in the home-ranges of the study animals. The sample size in parenthesis indicates the UBF tree species that have been surveyed: for chimpanzees, data source from [135]; for gorillas, data from vegetation transects of a previous study carried out by A.T. and S.M. (see Methods).
[b] *% UBF Ground Layers with Comparable Density of Usual Food*: percentage of UBF ground layer species consumed by the study animals that have either a comparable density (individuals/ha) of species usually consumed as food, or constitute usual food but for a different plant part. The sample size in parenthesis indicates the UBF ground layer species that have been surveyed: for chimpanzees, data source from [136] and [137]; for gorillas, see footnote a.
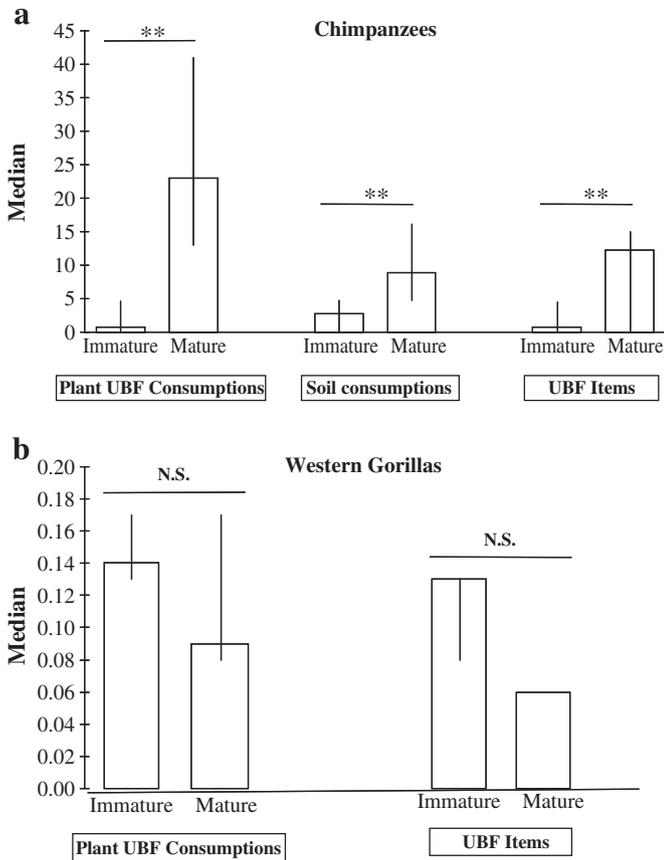
Fig. 2. a–b. Comparison of consumptions of UBFs (plants and soil) and number of UBF items consumed per each age class in chimpanzees (a) and gorillas (b). Given the low occurrence of soil consumption in gorillas (N = 2) this is not displayed in the graph. Medians are displayed as bold boxes, and quartiles (1st and 3rd) as bars. See text for statistical details.

Hypothesis 2. In terms of physiology and body size, larger individuals should tolerate higher amounts of secondary compounds and thus ingest UBFs more frequently.

When controlling for the number of days each individual was present in the party, older chimpanzees consumed UBF plants and soil more frequently than younger ones ($N_{Immature} = 16$, $N_{Mature} = 27$, median UBF plant consumption events: Immature = 0.80 $Q_{1-3} = 0.00-4.60$, Mature = 23.00 $Q_{1-3} = 13.00-41.00$, $z = -5.43$, $P \ll 0.001$; median soil consumption events: Immature = 2.80 $Q_{1-3} = 0.00-4.72$, Mature = 8.90 $Q_{1-3} = 4.81-16.07$, $z = -4.36$, $P = 0.002$; Fig. 2a). They also consumed a higher diversity of UBF items (median: Immature = 0.80 $Q_{1-3} = 0.00-4.55$, Mature = 12.30 $Q_{1-3} = 0.09-14.98$, $z = -4.42$, $P \ll 0.001$; Fig. 2a). Controlling per hour of focal sampling of each individual, the opposite pattern of consumption frequency although not significant was found in gorillas ($N_{Immature} = 6$, $N_{Mature} = 7$, median UBF plant consumption events: Immature = 0.14 $Q_{1-3} = 0.13-0.17$, Mature = 0.09 $Q_{1-3} = 0.08-0.17$, $U = 14.00$, $P = 0.317$; soil consumption occurred only within the immature class; Fig. 2b). Immature gorillas consumed also a larger variety of UBF items but not significantly so (Immature = 0.13 $Q_{1-3} = 0.08-0.13$, Mature = 0.06 $Q_{1-3} = 0.06$, $U = 11.00$, $P = 0.153$; Fig. 2b). In gorillas, but not in chimpanzees, larger bodied individuals consumed larger quantities of the same UBF item than smaller individuals (Wilcoxon test: chimpanzees, $T^+ = 2.00$, $N = 4$, $P = 0.273$; gorillas, $T^+ = 11.00$, $N = 11$, $P = 0.050$).

Hypothesis 3. Chimpanzees rely more on social learning than western gorillas.

Considering all occurrences of UBF consumption (N = 355), watching was involved in 38% of chimpanzee plant consumption events and 29% of soil consumption events (N = 155). In gorillas, watching occurred in 14% of UBF plant consumption events (N = 116), while none occurred during consumption of soil (N = 2). The mean number of observers per watching event was similar in chimpanzees (1.29; $range_{nb. observers} = 0-4$) and gorillas (1.43; 0–3). When controlling for the daily time spent consuming UBF plants by chimpanzees ($N_{UBF\ plant\ consumptions} = 145$) and gorillas ($N_{UBF\ plant\ consumptions} = 33$), watching frequency per day during consumption of UBF plants did not differ between the two species (median: chimpanzees = 0.00 $Q_{1-3} = 0.12-0.35$, gorillas = 0.00 $Q_{1-3} = 0.14-0.26$, $z = 0.29$, $P = 0.769$). However, in comparison to gorillas, chimpanzee consumers of UBFs were more often alone (chimpanzees: 72% of total of UBF consumptions, N = 351, range $N_{individual} = 0-6$; gorillas: 12%, N = 50, 0–11) and had less individuals (either observers or not) present within 15 m (median: chimpanzees = 1.00 $Q_{1-3} = 0.00-2.00$, gorillas = 3.00 $Q_{1-3} = 1.25-4.00$, $z = 6.53$, $P \ll 0.001$). Therefore, chimpanzees had a lower probability of being observed and of observing UBF consumptions when happening. Additionally, chimpanzees watched UBF consumers for longer ($N_{watching\ events} = 185$; median = 90.00 s $Q_{1-3} = 60.00-120.00$ s) than gorillas ($N_{watching\ events} = 20$; 17.50 s $Q_{1-3} = 9.25-32.50$ s, $z = 6.031$, $P \ll 0.001$).

Comparative data on all non-aggressive social interactions occurring during UBF and usual food consumptions in both species are summarized in Fig. 3a–b. When comparing frequency of watching between UBF and usual food feeding, watching occurred almost solely during consumption of UBFs in chimpanzees ($N_{UBF} = 162$ vs. $N_{Usual\ Food} = 1$), while in gorillas there is only a tendency to watch more during UBF feeding (median watching events per hour of UBF or
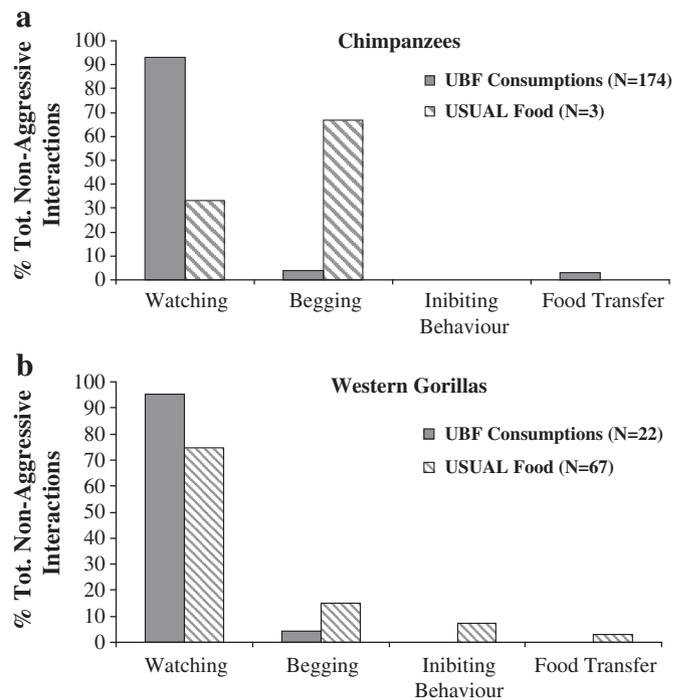

Fig. 3. a–b. Comparative summary of the total non-aggressive interactions in chimpanzees (a) and western gorillas (b) while feeding unusual and usual food items. *Watching* includes cases in which only observation was performed and it was not followed by any other interaction behaviors such as begging, inhibition or food transferring. *Inhibiting Behaviors*: all occurrences were taking (or "stealing") from hand without resistance from the consumer. *Food Transfer* includes cases in which food transferring occurred without begging behavior by the receiver. Sample size is displayed given the low occurrences of certain behaviors.

usual food feeding: UBF $= 0.33$ $Q_{1-3} = 0.06$–0.48; Usual food $= 0.02$ $Q_{1-3} = 0.01$–0.02; $T^+ = 1.00$, N $= 6$, P $= 0.079$). After watching an UBF consumption, gorilla observers fed more often (68% of watching events) than chimpanzee observers (27% of watching events) on the same food eaten by consumers ($N_{Chimpanzees} = 162$, $N_{Gorillas} = 22$, z $= -3.46$, P $\ll 0.001$), while no differences between the two ape species were found during usual food consumptions ($N_{Chimpanzees} = 3$, $N_{Gorillas} = 48$, z $= 0.54$, P $= 0.589$).

Co-feeding (of any UBF or usual food) within 15 m from the consumer occurred in 27% of UBF plant consumption events by a first consumer in chimpanzees (N $= 355$) and 42% in gorillas (N $= 52$). Both during UBF and usual food consumptions, all food transfer events were initiated by the receivers either by begging ($N_{Chimpanzees} = 2$; $N_{Gorillas} = 6$) or simply approaching the consumer ($N_{Chimpanzees} = 5$; $N_{Gorillas} = 2$). In chimpanzees two food transfers occurred between adult males, and all others between mother and offspring, while in gorillas all cases but two (mother–offspring) occurred within the immature class. Inhibition behaviors were absent in chimpanzees, while in gorillas all such events (N $= 5$) corresponded to mothers taking usual food away from the hand of the offspring ($N_{Infants} = 4$; $N_{Juvenile} = 1$) and consuming it, and thus was related to feeding dominance of mothers rather than learning processes (Fig. 3a–b).

Begging occurred infrequently in both species both during UBF ($N_{Chimpanzees} = 7$; $N_{Gorillas} = 1$) and usual food consumptions ($N_{Chimpanzees} = 2$; $N_{Gorillas} = 10$; Fig. 3a–b). Begging was successful (the beggar succeeded to obtain the desired food after begging) in 45% of all chimpanzee begging cases ($N_{Tot} = 9$) and 91% of gorilla' cases ($N_{Tot} = 11$). For chimpanzees, successful begging occurred either as transfers both of UBFs (N $= 1$) and usual food (N $= 2$) from the consumer to the beggar or by eating the wadge of an UBF left on the ground by the consumer (N $= 1$). For gorillas, successful begging occurred not only as voluntary food transfers ($N_{UBFs} = 1$, $N_{Usual\ Food} = 5$) but also as stealing — involuntary food transfers — ($N_{Usual\ Food} = 3$) or simply by searching and finding the same food type around the consumer ($N_{Usual\ Food} = 1$).

Hypothesis 4. If observation of conspecifics is related to learning, younger individuals observe more frequently than older (experienced) individuals, who instead play a role as demonstrators.

In chimpanzees no differences were found in watching frequency between the two age classes ($N_{Immature + Sub-Adult\ Females} = 22$, $N_{Mature} = 21$) both during the consumption of UBF plants (median of watching frequency: "Immature + sub-adult females" 7.12 $Q_{1-3} = 0.00$–15.44, Mature $= 10.28$ $Q_{1-3} = 7.06$–14.03, z $= 0.68$, P $= 0.272$) and soil ("Immature + Sub-Adult Females" $= 0.19$ $Q_{1-3} = 0.00$–0.49, Mature $= 0.44$ $Q_{1-3} = 0.31$–1.23, z $= 1.50$, P $= 0.136$). In contrast immature gorillas observed conspecifics more frequently than mature individuals ($N_{Immature + Sub-Adult\ Females} = 8$, $N_{Mature} = 5$; median: "Immature + Sub-Adult Females" $= 0.04$ $Q_{1-3} = 0.03$–0.06, Mature $= 0.00$ $Q_{1-3} = 0.00$–0.03; z $= 2.34$, P $= 0.019$). In chimpanzees the majority of watching events occurred from "Immature + Sub-Adult Females" class to the Mature class (54%, N $= 140$) and within the Mature class (39%). When considering only immature individuals who had their mother still present in the community (N $= 11$) 48% of their total observations (N $= 83$) were directed towards their mothers. Moreover among the immatures, infants (N $= 5$) watched their mother in 89% of their observations (N $= 35$). In contrast, in gorillas the majority of watching events typically occurred within the "Immature + Sub-Adult Females" class (70%, N $= 20$) and most demonstrators were related to their observers (91%, N $= 22$), principally half siblings.

During consumption of UBF plants and soil, mature chimpanzees were observed more often than immature chimpanzees (median UBF consumption events with observers: "Immature + Sub-Adult Females" $= 0.00$ $Q_{1-3} = 0.00$, Mature $= 11.00$ $Q_{1-3} = 8.37$–17.81, z $= 39$, P $\ll 0.001$; median soil consumption events with observers:

"Immature + Sub-Adult Females" $= 0.00$ $Q_{1-3} = 0.00$, Mature $= 0.89$ $Q_{1-3} = 0.00$–1.46, z $= 98.00$, P < 0.001), while no differences were found in gorillas ("Immature + Sub-Adult Females" $= 0.03$ $Q_{1-3} = 0.00$–0.05, Mature $= 0.01$ $Q_{1-3} = 0.00$–0.01, U $= 13.00$, P $= 0.305$). Moreover, in chimpanzees the frequency of UBF consumptions with observers follows a significant quadratic relationship with age of the consumer: reaching a maximum for consumers of 29–30 years old and decreasing for individuals older than 35 years old (Linear Regression with quadratic effect: multiple $r^2 = 0.627$, F $= 17.66$, $P_{age\ consumer} \ll 0.001$, $P^2_{(age\ consumer)} < 0.001$; Fig. 4). Given that most of the ages of the gorilla group members were unknown, this finer analysis was not possible for the gorillas.

4. Discussion

4.1. Frequency of UBF consumption is higher in chimpanzees than in western gorillas

The majority of UBF species consumed by chimpanzees were abundant in their home range or have comparable densities with usual food species, suggesting that the consumption of rare foods may be linked to reasons other than nutrition, such as self-medication as previously proposed [10]. For western gorillas results are less straightforward. Some UBF plant species of gorillas were rare in their habitat, suggesting that unusual consumption of some UBF species may be linked to low availability, and thus for nutritional benefits rather than medicinal ones. However, other gorilla UBF species were 1) common in the environment, 2) included in the usual diet but for different plant parts, and 3) of high availability considering the item consumed (leaves, dry leaves, barks, seeds, fruit) relative to the lower availability of the plant itself, and 4) with clear low nutritional value (such as soil, dry leaves, barks, and/or considering the small amount ingested). This suggests that in western gorillas consumption of unusual food may not always be the result of low availability but may also be linked to specific pursuit of an item for reasons other than nutrition [141].
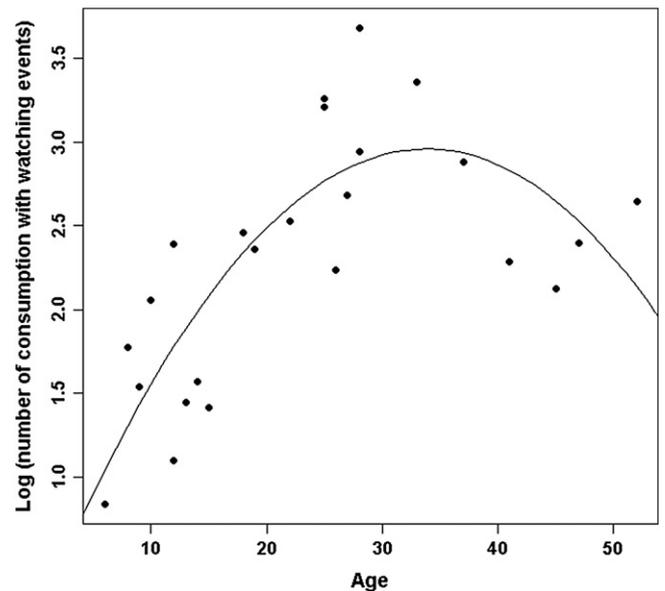

Fig. 4. Quadratic relationship between the number of consumptions with watching events per individual and the age of consumers in wild chimpanzees. Individuals who were neither observers nor consumers (e.g. 10 individuals for whom interactions where more difficult to observe: four new-borns, five immigrating adolescent females and one 9 year-old who was caught in a snare on two feet) were excluded from the linear regression analysis. Estimated coefficients: intercept $= 0.122$ Std. Error $= 0.392$, Age $= 0.168$ Std. Error $= 0.033$, Age$^2 = -0.002$ Std. Error $= 0.001$.

As predicted, chimpanzees consumed UBF plants and soil twice as frequently as western gorillas. In contrast to chimpanzees, the more diverse and herbivorous diet and gut specialization with greater detoxification abilities [28,31,70,142] probably allow western gorillas to ingest more secondary compounds per day, alongside bioactive substances, to maintain their health. In comparison, the mainly frugivorous chimpanzees may need to balance their diet with prophylactic plants beneficial for health but ingest them in lower amount to avoid toxicity. These opposing needs may have led chimpanzees and their common ancestors with humans to consume bioactive plants specifically in association with certain stimuli (e.g. malaise and diseases) creating the subtle differences between food and medicine which become more precise in modern humans [3]. Our results on geophagy strengthen the hypothesis that, similar to some human cultures, soil consumption may allow chimpanzees to improve their detoxification abilities, lacking in their general physiology, helping also to increase availability of bioactive compounds (chimpanzees: [19]; humans: [3,134,143]). In addition, given the higher level of sociality (e.g. social grooming, meat sharing) and the size of their communities, chimpanzees may be more susceptible than western gorillas to intra-group (epidemic) disease and parasite transmission (but see [144] for inter-group transmission). Further chemical analysis will help us to test the alternative hypothesis that UBF items (with low nutritional and energetic values) may be an important supply of specific micronutrients (vitamins, minerals) rare in the environment [145,146].

4.2. Frequency of consumption of UBFs is different between body size classes and the two ape species

In contrast to immature individuals, adult chimpanzees consumed a wider diversity of UBF items and more frequently, while in gorillas this difference was not significant. These findings support the hypothesis that in chimpanzees UBF items may contain potentially toxic bioactive substances resulting in higher consumption by larger individuals who have greater toxin tolerance and greater experience in selecting a wider range of plant parts. On the contrary, sampling of UBFs in young western gorillas likely reflects the random sampling of plants during the process of the adult diet acquisition [147]. In addition, the finding that in western gorillas, but not in chimpanzees, larger bodied individuals consumed a greater quantity of UBF items strengthens the hypothesis that in western gorillas a proportion of unusual foods consumed may be ingested for nutritional purposes rather than for their potential pharmacological properties, since larger individuals generally require a greater amount of food to sustain their larger size [148]. The absence of this pattern in chimpanzees may suggest that the severity of symptoms, rather than periodical health maintenance, may confound posology leading to consumption of different quantities according to specific needs, but further studies are needed to confirm this hypothesis.

4.3. Chimpanzees rely more on social learning than western gorillas

During consumption of UBFs no differences were found between the two species in the frequency of watching behavior nor in the number of observers. However, in contrast to western gorillas, chimpanzees seemed to take more advantage of having a "demonstrator" close to them as they: 1) had less opportunity to observe conspecifics while feeding on UBF items, 2) watched conspecifics typically only in association with UBF consumption and not with usual food consumption, and 3) observed consumers for longer bouts. Additionally, chimpanzees seemed to be more cautious than gorillas in consuming UBF items even after observing other conspecifics consuming them. In a parallel study carried out in captivity by the same authors [149], chimpanzees engaged in longer investigation and pre-ingestion time than western gorillas when presented with the same set of novel aromatic plants.

The higher cautiousness and reliance on social interactions in chimpanzees during consumption of UBFs may suggest that selection of these items may be dangerous and complex for chimpanzees while

gorillas may individually discover curative plants in a less risky fashion by sampling them more safely [10,150]. However, western gorillas may also acquire feeding information (both for nutrition and self-medication) just being in proximity with other individuals like shown for other animal species [151] rather than by evident observational learning, more challenging for them given the lower social tolerance within group respect to chimpanzees.

Our results are consistent with previous observations of great apes relying more on observational learning in association with food characteristics that are difficult to learn independently (rare foods or those requiring extraction [41]). However, reasons for and consequences of watching events seem to be different in the two apes. When the UBF item was available after the consumer's departure, western gorilla observers consumed the same item more often than chimpanzees, possibly for nutritional reasons or simply because the consumption was a safe behavior for the consumer. In contrast, chimpanzees may have watched conspecifics with the aim of knowledge acquisition (Fig. 4): health and physiological conditions of the consumers (and observers) may determine the consumption or avoidance of the same UBF item. Begging behavior may be also used by these two great ape species as supplementary means to gather information on the appearance and taste of food consumed by other individuals, even though it occurred rarely.

Contrary to what has been shown in captive monkeys and humans for diet acquisition, synchronized feeding did not enhance consumption of UBFs in the two apes, particularly in chimpanzees, suggesting either an association of unusual food consumption with specific disease symptoms or that observational learning of the same item may be required for decreasing the risk of unusual or complex food consumption [21,41,152–154]. In both great ape species, food transfer was too rare during both usual and unusual food consumption to be an important means in promoting learning in all great ape species, as previously suggested by [54].

Our results on social non-aggressive interactions in food contexts suggest that differences in physiological capabilities and sociality between chimpanzees and gorillas may influence mechanisms of food knowledge acquisition. Anecdotes on chimpanzees, such as mothers providing bark pieces or tools to offspring, or bending stems for them ([155], Krief pers. observ.), suggest that social facilitation may be a stronger trait in chimpanzees than in western gorillas. Unusual food consumption may be more dangerous and complex for chimpanzees and thus more dependant on social learning, while a balance of individual and social learning may be more optimal in the more cohesive groups of western gorillas who consequently also experience higher within-group feeding competition [66,156].

4.4. In chimpanzees older individuals play a demonstrator role, while immature western gorillas acquire food information from other immatures

First, observational learning occurs in chimpanzees during the entire life of an individual as shown by the absence of differences in watching rate between the classes, while in western gorillas it seems to be a typical trait of immatures and adolescent females. The higher level of social tolerance in feeding contexts in chimpanzees compared to western gorillas [62,157], may allow chimpanzees of all age classes to watch consumers closely and thus acquire food information. In fact, many watching events occurred within mature individuals and only half of the observations made by immature chimpanzees were directed towards their mother. In contrast to chimpanzees, western gorillas are more protective of their food ([149], Masi pers. observ.) not permitting or possibly avoiding close approaches by other individuals (except for closely related individuals or clearly dominant ones — e.g. the silverback). This difference between chimpanzees and gorillas explains the high frequency of watching in gorillas among related individuals and particularly among immatures (who are all half-siblings) leading to a more relaxed feeding competition compared to that between adults or

unrelated individuals. Second, the more frugivorous diet of chimpanzees may cause them to balance the tendency throughout their lives to search for alternative food when fruit is scarce, with the need to be cautious due to lack of physiological resistance [31,70].

Finally, like humans and other primates, chimpanzees seem to follow the strategy of "copying successful individuals" with some individuals being copied more often than others [158–160]. In fact, the best demonstrators in chimpanzees were adults before senescence who probably have higher rank, better fitness and health than the youngest or oldest adults (Fig. 4).

4.5. Conclusions and perspective for understanding human evolution

Since gorillas are phylogenetically more distant from humans than chimpanzees, and differ more in their physiology and level of sociality, this comparative study provides a new contribution in understanding the roles that both social complexity and detoxification abilities have played in the origins of traditional medicine and self-medication in humans. Results of this study suggest that reasons for the consumption of plants with bioactive properties other than nutrition may have appeared on the evolutionary timescale in association with greater level of social tolerance and flexibility, and lack of herbivorous gut specialization which was probably absent in the common ancestors of humans and chimpanzees [150].

The results of this study highlight potentially different roles of observational learning in the two ape species. They suggest a major role of horizontal knowledge transmission among immature gorillas, and surprisingly show a strong influence of individuals other than mothers in the learning process — similar to that found among children over 5 years in some human hunter-gather populations [161]. In western gorillas unusual feeding behaviors are learnt before adulthood since they are probably part of their diet. On the contrary, in highly social apes like chimpanzees, information on unusual feeding is continually acquired even after having achieved the adult diet, likely linked to reasons other than nutrition. In contrast to western gorillas, chimpanzees seem to rely more on vertical transmission copying older and fitter individuals [158,159].

Further studies are needed to gain a better understanding of the interrelation between plant choice and food knowledge acquisition by the great apes with regards to nutritional and medicinal properties of plants and the health of consumers.

Acknowledgments

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