

How do great apes acquire information on unusual feeding behaviors? A window to understand origins of self-medication in humans

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Introduction

Chimpanzees are known to consume some plants with low nutritional value and high bioactive compounds possibly to maintain and improve their health suggesting a self-medicating role (e.g. Huffman, 2003). How the great apes learn to consume bioactive plants has been little investigated.

Primates evolved neophobia (reluctance) towards novel foods (Visalberghi and Fragaszy, 1995) probably in parallel, but independently, of the unpalatable taste of certain plant parts (e.g. bitter taste) indicating the presence of toxic secondary compounds (Freeland and Janzen, 1974). Similar to our modern drugs, if certain secondary substances are ingested in small quantities they can have beneficial effects towards maintaining health (Krief et al., 2006).

The balance between beneficial and toxic effects also depend on the animal's body size and physiology (ability to detoxify toxins; Freeland and Janzen, 1974). Varying physical and physiological tolerances towards toxicity may thus lead to different levels of neophobia (Visalberghi et al., 2003).

The higher is the level of sociality of a taxon, the more learning animals can overcome the adaptive reluctance to novelty relying on social information (e.g. co-foraging and observational learning; Agostini and Visalberghi, 2005).

While chimpanzees (*Pan troglodytes*) remain mainly frugivorous throughout the year (Tutin and Fernandez, 1993) the longer gut retention time and enlarged hindgut with more cellulose-digesting ciliates (Chivers and Hladik, 1980) allow gorillas (*Gorilla gorilla*) to digest foods high in fibre and toxins, and to shift to a herbivorous diet when fruit is scarce (Rogers et al., 2004; Masi et al., 2009). Moreover, while chimpanzees develop foraging tools relying on social learning (e.g. Ueno and Matsuzawa, 2005; Lonsdorf, 2006; Boesch, 1991), it is not clear whether gorillas develop such "traditions" (Byrne et al., 2011; Masi, 2011) or rely on a mixture of genetic predisposition and individual learning (Tennie et al., 2008).

This study focus on ape consumption of "unusual" foods, food that is rarely fed upon with low energetic/ nutritional content and/or known bioactivity. If an unusual food is toxic and consumed for other reasons than nutrition (e.g. disease), we predict: 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 than smaller individuals. If consumption of unusual food is socially learnt we expect 3) a higher frequency of inter-individual observations among the highly social chimpanzees than in gorillas and 4) immature individuals watching more frequently older individuals, who play a role as demonstrators.

Material and Methods

Chimpanzee data were collected every 15 minutes (January-August 2008, October-December 2008) by S.K. and field assistants on a habituated community (41-44 individuals) at Kanyawara, in the north-west of Kibale National Park, Uganda ($N_{\text{Days}}=237$, $N_{\text{Hours}}=2000$). Focal animal sampling of all age/sex classes was carried out at Bai-Hokou by S.M. (April-July 2008, November 2008-March 2009) on a habituated group of western gorillas ($N=11-13$) in the Dzanga-Ndoki National Park, Central African Republic ($N_{\text{Days}}=214$, $N_{\text{Hours}}=818$).

A list of unusual and bioactive foods (UBF), defined as rarely eaten food items, was established on the base of low consumption frequency, low energetic value, results of bioassays, phytochemical literature and/or traditional uses in local medicine. Individuals present within 15m from consumers were recorded at each UBF consumption.

All occurrences of watching behaviour of food consumers and the duration of this event were recorded whilst feeding on both usual and unusual food.

When investigating the possible influence of body size on the consumption of UBFs, the individuals were pooled in two broader classes: 1) immature size individuals (juveniles and infants) and 2) mature size individuals (adults and sub-adults). To investigate the effect of age on social learning we modified the classes considering that: 1) overall infants, juveniles and sub-adults are expected to have a lower degree of neophobia with respect to adults, and 2) males do not disperse at adulthood in chimpanzees and in gorillas males emigrate at least five years later than females. Therefore, sub-adult females were moved into the immature class.

Results

Daily frequency of UBFs consumption (F_{UBF}) was twice as high in chimpanzees as in gorillas (F_{UBFs} : 0.27 vs. 0.14; Mann-Whitney U, $N_{Chimpanzees}$ = 232, $N_{Gorillas}$ = 214, z = -8.45, P << 0.001; Fig. 1). While older chimpanzees consumed UBF plants more frequently than younger ones ($N_{Immature}$ = 16, N_{Mature} = 27, median UBF plant consumptions: Immature = 0.80 Q_{1-3} = 0.00-4.60, Mature = 23.00 Q_{1-3} = 13.00-41.00, z = -5.43, P << 0.001; Fig. 1a), no differences were found in gorillas ($N_{Immature}$ = 6, N_{Mature} = 7, 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; Fig. 1b). Watching frequency

per day during consumption of UBF plants did not differ between the two species (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). In comparison to gorillas, chimpanzee consumers of UBFs were 1) more often alone (chimpanzees: 72% of total of UBF consumptions, N = 351, range N = 0-6; gorillas: 12%, N = 50, 0-11), 2) less individuals present within 15m (chimpanzees = 1.00 Q_{1-3} = 0.00-2.00, gorillas = 3.00 Q_{1-3} = 1.25-4.00, z = 6.53, P << 0.001), and were watched for longer bouts (Chimpanzees: N = 185; median = 90.00 sec Q_{1-3} = 60.00-120.00 sec; Gorillas: N = 20; 17.50 sec Q_{1-3} = 9.25-32.50 sec, z = 6.031, P << 0.001). During UBF plant consumptions, no differences were found in watching frequency between the two age classes ($N_{Immature + Sub-Adult Females}$ = 22, N_{Mature} = 21) in chimpanzees (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). In contrast immature gorillas observed conspecifics more frequently than mature individuals ($N_{Immature + Sub-Adult Females}$ = 8, N_{Mature} = 5; "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 immatures towards matures (54%, N = 140) and within matures (39%), while in gorillas within immatures (70%, N = 20). In chimpanzees consumers of 29-35 years old were the most observed (Linear Regression with quadratic effect: multiple r^2 = 0.627, F = 17.66, << 0.001, $P_{(age\ consumer)}$ 2 < 0.001; Fig. 2).

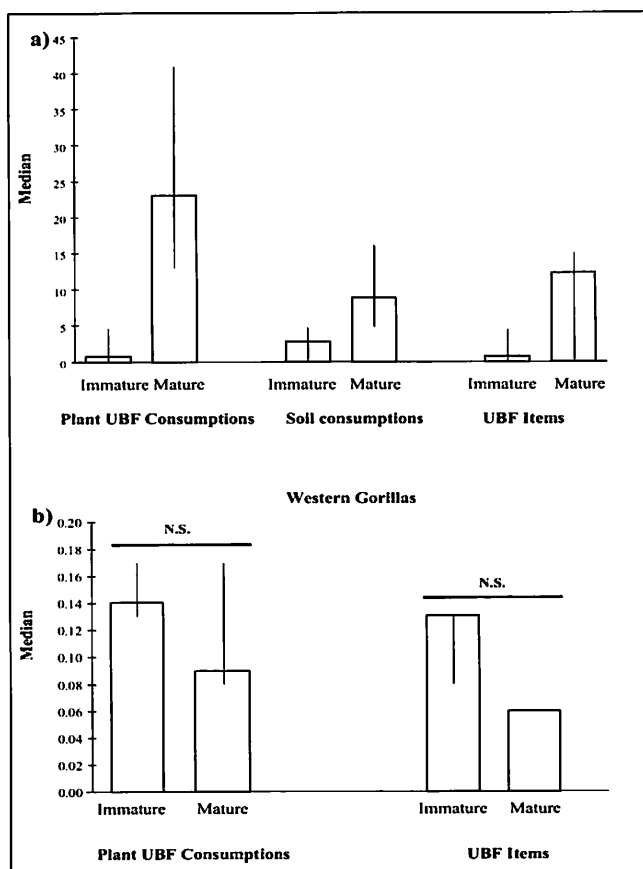


Fig. 1 a-b. Comparison of UBF consumptions and number of items consumed per age class in chimpanzees (a) and gorillas (b). Bold boxes: medians; bars: 1st and 3rd quartiles.

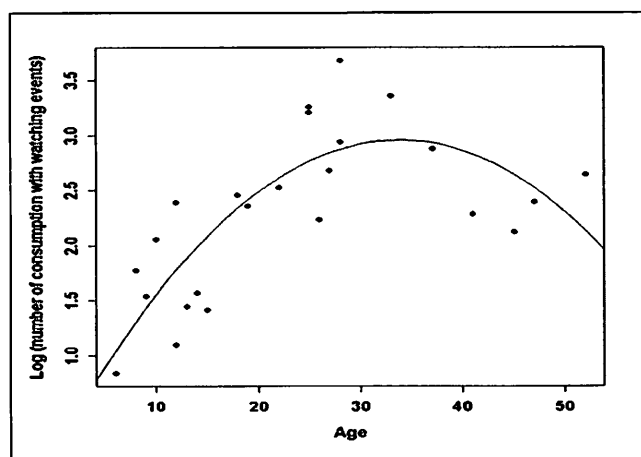


Fig. 2. Quadratic relationship between the number of consumptions with watching events per individual and the age of consumers in wild chimpanzees.

Discussion

Chimpanzees consumed UBFs twice as frequently as western gorillas. In contrast to chimpanzees, the more diverse and herbivorous diet and gut specialization with greater detoxification abilities (Chivers and Hladik, 1980) 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 in association with certain stimuli (e.g. malaise) originating the subtle differences between food and medicine (Johns, 1990).

In contrast to immature individuals, adult chimpanzees consumed more frequently UBF items, while in gorillas this difference was not significant. The potentially higher content of toxic bioactive substances may explain the higher UBF consumptions by larger individuals who have greater toxin tolerance in chimpanzees. Sampling of UBFs in young western gorillas likely reflects random sampling of plants during adult diet acquisition (Watts, 1985).

No differences were found between the two species in the frequency of watching behavior nor in the number of observers per consumer. However, chimpanzees seemed to take more advantage than gorillas of having a "demonstrator" close to them as they: 1) had less opportunity to observe conspecifics while feeding on UBFs, 2) watched conspecifics in association with UBF consumption and not with usual food, and 3) observed consumers for longer bouts. The higher cautiousness and reliance on social interactions of chimpanzees during consumption of UBFs suggest UBF selection may be more dangerous or complex.

Observational learning occurs in chimpanzees during the entire life of an individual, 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 (Masi *et al.*, 2011), may allow them to acquire information watching closely consumers of all age classes, particularly adults before senescence with better fitness and health. Since western gorillas are more protective of their food (Masi pers. observ.), watching among immatures may result from a more relaxed feeding competition.

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 (Milton, 1999). This study highlights also potentially different roles of observational learning in the two apes: 1) a major role of horizontal knowledge transmission in gorillas similar to that found among children in some human hunter-gather populations (Mingot, 2000), and 2) a major role of vertical transmission in highly social chimpanzees who continually acquire feeding information throughout their life following like humans the strategy of "copying successful individuals" (Laland, 2004)

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