



Leaf Surface Roughness Elicits Leaf Swallowing Behavior in Captive Chimpanzees (*Pan troglodytes*) and Bonobos (*P. paniscus*), but not in Gorillas (*Gorilla gorilla*) or Orangutans (*Pongo abelii*)

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Abstract Researchers have described apparently self-meditative behaviors for a variety of nonhuman species including birds and primates. Wild chimpanzees, bonobos, and gorillas have been observed to swallow rough leaves without chewing, a behavior proposed to be self-meditative and to aid control of intestinal parasites. Researchers have hypothesized that the presence of hairs on the leaf surface elicits the behavior. We investigated the acquisition and the underlying mechanisms of leaf swallowing. We provided 42 captive great apes (24 chimpanzees, six bonobos, six gorillas, and six orangutans) with both rough-surfaced and hairless plants. None of the subjects had previously been observed to engage in leaf swallowing behavior and were therefore assumed naïve. Two chimpanzees and one bonobo swallowed rough-surfaced leaves spontaneously without chewing them. In a social setup six more chimpanzees acquired the behavior. None of the gorillas or orangutans showed leaf swallowing. Because this behavior occurred in naïve individuals, we conclude that it is part of the behavioral repertoire of chimpanzees and bonobos. Social learning is thus not strictly required for the acquisition of leaf swallowing, but it may still facilitate its expression. The fact that apes always chewed leaves of hairless control plants before swallowing, i.e., normal feeding behavior, indicates that the surface structure of leaves is indeed a determinant for initiating leaf swallowing in apes where it occurs.

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Introduction

Humans harvest plants for medicative purposes. Such adaptive antiparasitic behaviors have their roots deep within the animal kingdom (Baker 1996; Clark and Mason 1985; Huffman 1997, 2003; Morrogh-Bernard 2008), and great apes are thought to ingest plant materials for medicinal reasons (Huffman 2001). An open question is how apparently self-meditative behaviors are acquired within a lifetime. Social transmission is required for the complex medical practices that characterize human societies, but it is unknown whether this is also true for other great apes.

When eating leaves, great apes normally chew many leaves at the same time before swallowing the resulting mass. In the case of several plant species, however, some species take only one leaf at a time and then fold it deliberately—and slowly—using a combination of tongue, lips, and palate before swallowing it without chewing (Fig. 1). One consequence of this is that the leaves can often be found whole, folded and undigested in the feces. After the first observations of leaf swallowing in Eastern chimpanzees (*Pan troglodytes schweinfurthii*) (Wrangham 1977; Wrangham and Nishida 1983), researchers have described leaf swallowing for the other chimpanzee subspecies (*P. t. verus*: Boesch 1995; *P. t. troglodytes*: Huffman 1997; *P. t. vellerosus*: Fowler *et al.* 2007) and bonobos (*P. paniscus*: Dupain *et al.* 2002; Huffman 1997), as well as Eastern lowland gorillas (*Gorilla beringei graueri*: Yamagiwa *et al.* 2005). There are no records of leaf swallowing in wild orangutans (*Pongo* spp.).

Huffman's (2001) review of the literature identified 34 different plant species that have been associated with leaf swallowing at several great ape study sites across Africa. Because these different plants all have rough-surfaced leaves (Huffman 1997, 2001; *cf.* Boesch 1995 for two exceptions) and there is no strong evidence for a chemically explanation for leaf swallowing (Huffman *et al.* 1996; Messner and Wrangham 1996; Ohigashi *et al.* 1991; Page *et al.* 1992, 1997), Huffman (1997,

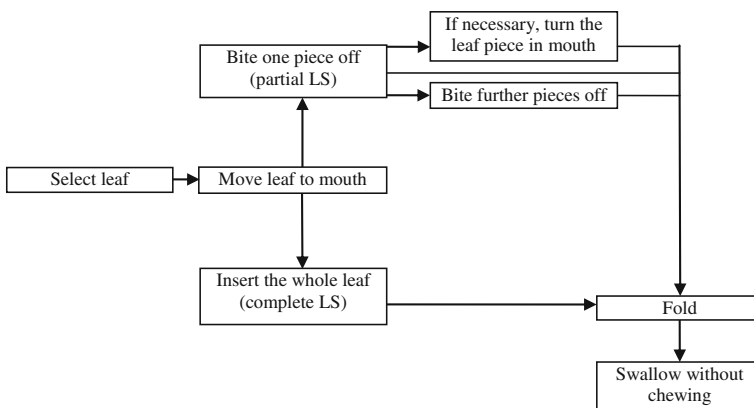


Fig. 1 One leaf swallowing event according to descriptions by Huffman *et al.* (2010). LS = leaf swallowing.

2001) suggested that the roughness of the leaves, rather than their chemical composition, was responsible for the appearance of leaf swallowing in apes. Huffman and Caton (2001) suggested that un-chewed leaves with a rough surface cause physical irritation that increases motility and secretion in an empty stomach and gut. This may in turn produce temporary diarrhea, thus expelling intestinal parasites. However, it is possible that relatively ordinary herbal substances and the roughness of leaves act together against parasites.

Leaf swallowing is assumed to be therapeutic when an individual infected with certain intestinal parasites and/or suffering abdominal pain exhibits the behavior (Huffman 2001). However, not all observations support the assumption that animals that swallow leaves are actually ill, because researchers have often not detected any evidence of illness or infection when leaf swallowing took place (chimpanzees: Boesch 1995; Wrangham and Goodall 1989; Wrangham and Nishida 1983; bonobos: Fowler and Fruth unpub. data). Although these observations potentially weaken the medical hypothesis, leaf swallowing rates do increase during times of high infection rates (chimpanzees: Huffman *et al.* 1997; Wrangham 1995; Wrangham and Nishida 1983; bonobos: Dupain *et al.* 2002; Fowler *et al.* 2007). This implies that leaf swallowing not only appears during acute illness, but may also be prophylactic (Hart 2005).

Researchers have proposed leaf swallowing behavior to be socially transmitted and have assumed that observational learning plays an important role for the acquisition of this behavior (Boesch 1995; Huffman and Wrangham 1994; Nishida *et al.* 1999). However, the fact that at least three ape species show leaf swallowing across Africa (Huffman 1997) suggests a genetic predisposition for the behavior. If a naïve individual spontaneously shows a behavior without ever having seen it demonstrated socially, this behavior may be due to a combination of environmental pressures (or affordances) and genetic predispositions, but it is arguably not cultural in the sense that its form requires or presupposes cultural transmission (Tennie and Hedwig 2009). Two studies in which several naïve healthy chimpanzees swallowed rough-surfaced plant leaves spontaneously without chewing showed that social learning was not necessary for the acquisition of leaf swallowing in captive chimpanzees (Huffman and Hirata 2004; Huffman *et al.* 2010). For us, these are latent solution experiments (Tennie and Hedwig 2009).

Although social learning is unnecessary to explain the form of a behavior, it may still play a role in influencing its distribution and frequency (Tennie *et al.* 2009). Huffman *et al.* (2010) found that social learning influenced the way the chimpanzees swallow the offered leaves (partial *vs.* complete leaf swallowing, Fig. 1). In addition, differences in the selection of plants for leaf swallowing between chimpanzee groups (Huffman 1997; Huffman and Hirata 2003; Nishida *et al.* 1999) may also be socially transmitted. However, several mechanisms besides high-fidelity social learning can lead to the selection of the same plant by different populations (Whiten and Ham 1992; Whiten *et al.* 2004).

We investigated mechanisms of leaf swallowing and its acquisition by providing 42 captive apes with two rough-surfaced and three hairless (control) plants. To investigate the role of social learning in the acquisition of leaf swallowing we tested naïve subjects individually and in the presence of conspecifics. If leaf swallowing is genetically predisposed, the characteristics of the plant and individual learning should be sufficient to trigger this behavior, and at least some captive African great ape subjects should exhibit leaf swallowing in a way similar to that observed in the wild.

We did not expect spontaneous leaf swallowing to occur in orangutans because there are no descriptions of it in wild populations. However, an absence of an observation of leaf swallowing in orangutans does not mean that it does not occur in this species. Based on previous studies, we predicted that social learning is not necessary for the acquisition of leaf swallowing in captive chimpanzees (Huffman and Hirata 2004; Huffman *et al.* 2010). In addition, we predicted that subjects would swallow rough-surfaced, but not hairless, leaves because wild African great apes prefer rough-surfaced leaves for leaf swallowing (Huffman 1997, 2001). Because older chimpanzees are more conservative in their feeding patterns (Nishida *et al.* 1983), we expected a negative relationship of age and leaf swallowing occurrence. Assuming a self-medicative function of leaf swallowing, we predicted that apes infected with parasites would be more likely to swallow leaves than uninfected subjects.

Materials and Methods

Subjects

We tested 42 captive great apes housed at the Wolfgang Köhler Primate Research Centre, Leipzig Zoo, Germany (Table I), including 24 chimpanzees (*Pan troglodytes*), six bonobos (*P. paniscus*), six gorillas (*Gorilla gorilla gorilla*), and six orangutans (*Pongo abelii*), with five different plant species (Table II).

We give the experimental sequence for each subject in Table IV. All subjects except one female gorilla, Bebe, were captive born. Before this study, their keepers had never observed the apes swallowing leaves without chewing them. We thus considered them naïve. All but one chimpanzee (Unyuro, a 13-yr-old male) lived in either a big group consisting of 18 individuals headed by an alpha male (Frodo, 16 yr old) or a small group composed of five females and a subordinate male (Alex, 9 yr old).

The seminatural indoor and outdoor enclosures of all apes were equipped with trees, ropes, and various enrichment items. All focal subjects were fed a diet of fruit, vegetables, leafy twigs, and monkey chow. None of the subjects was water or food deprived at any time. All apes participate regularly in noninvasive cognitive studies. Animal husbandry and research comply with the EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria, the WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums, and the Guidelines for the Treatment of Animals in Behavioral Research and Teaching of the Association for the Study of Animal Behavior (ASAB). The research adhered to all German laws regarding animal testing and holding.

Keepers regularly investigated the feces of the apes visually for parasites. If infection was suspected, the veterinarian conducted an examination for parasite eggs. The big chimpanzee group ($N=17$), the bonobos ($N=6$), the orangutans ($N=6$), and one male chimpanzee (Unyuro) were all diagnosed with intestinal parasites (roundworms) at some point during the study. Once or twice a year and after diagnosis the apes are administered with a worm treatment. The chimpanzees in the big group and the bonobos were treated two months before the beginning of the tests. Unyuro and the orangutans were treated during the course of this study. The keepers assessed that

Table 1 Overview of subjects

Species	Name	Sex	Age	Group	Mother	Father	Rearing
Chimpanzee	Bangolo	m	1	Big	Dorien	Unkown	Parent
	Corrie	f	33	Big	Debbie	Izzak	Hand reared
	Dorien	f	29	Big	Diana	Fritz	Hand reared
	Fraukje	f	34	Big	Louise	Unknown	Hand reared
	Frodo	m	16	Big	Natascha	Robert	Parent
	Kara	f	5	Big	Fraukje	Unkown	Parent
	Kofi	m	5	Big	Ulla	Unkown	Parent
	Lobo	m	6	Big	Corrie	Robert	Parent
	Lome	m	8	Big	Corrie	Robert	Parent
	Natascha	f	30	Big	Regina	Fritz	Hand reared
	Patrick	m	13	Big	Corrie	Robert	Parent
	Pia	f	10	Big	Fraukje	Robert	Parent
	Riet	f	32	Big	Marco	Anita	Hand reared
	Robert	m	34	Big	Gina	Jacob	Hand reared
	Sandra	f	17	Big	Riet	Robert	Parent
	Swela	f	14	Big	Benga	Eros	Parent
	Tai	f	7	Big	Riet	Robert	Parent
	Ulla	f	33	Big	Yvonne	Izzak	Hand reared
	Alex	m	9	Small	Agathe	Arthur	Hand reared
	Alexandra	f	10	Small	Phil	Tom	Hand reared
	Annett	f	10	Small	Jana	Bram	Hand reared
	Fifi	f	17	Small	Ulla	Robert	Parent
	Gertudia	f	17	Small	Corrie	Robert	Parent
Jahaga	f	17	Small	Fraukje	Robert	Parent	
Unyuro	m	13	Separate	Tana	Eros	Parent	
Bonobo	Fimi	f	2		Yasa	Unknown	Parent
	Joey	m	27		Dzeeta	Desmond	Hand reared
	Kuno	m	13		Kombote	Maskini	Hand reared
	Limbuko	m	14		Lina	Masikini	Hand reared
	Loto	m	0.5		Ulindi	Unknown	Parent
	Luiza	f	5		Ulindi	Limbuko	Parent
	Ulindi	f	16		Natalie	Bono	Parent
	Yasa	f	12		Diatou	Kakowet II	Parent
Gorilla	Bebe	f	30		Wild	Wild	Parent until capture
	Gorgo	m	29		Boma	Massa	Hand reared
	Kibara	f	6		Viringika	Gorgo	Parent
	Louna	f	4		Bebe	Gorgo	Parent
	Viringika	f	15		Inge	N'Gola	Parent
	Zola	f	2		Viringika	Gorgo	Parent
Orangutan	Batak	m	0.75		Pini	Bimbo	Parent
	Bimbo	m	29		Noni	Major	Hand reared
	Dokana	f	21		Djudi	Djeruk	Parent

Table I (continued)

Species	Name	Sex	Age	Group	Mother	Father	Rearing
	Kila	f	10		Dunja	Tuhjo	Parent
	Maia	f	2		Dunja	Bimbo	Parent
	Padana	f	12		Pini	Walther	Parent
	Pini	f	22		Dunja	Coco	Parent
	Raja	f	6		Pini	Walther	Parent
	Suaq	m	1		Padana	Bimbo	Parent
	Tanah	f	1		Dokana	Bimbo	Parent






f = female; m = male; age in years at the beginning of the study

because of regular veterinary treatment, the subjects were not strongly influenced by this natural infection.

Plants

Plants used in this study (Table II) 1) were nontoxic and 2) novel to the apes; 3) had no known chemical compounds affecting the gastrointestinal tract; and 4) were abundantly available during the study. We used topinambur* (*Helianthus tuberosus*) (experimental/hairy plants are indicated with an asterisk), the same species used by

Table II Overview of plants used

Latin name	<i>Helianthus tuberosus</i>	<i>Beta vulgaris</i> ssp. <i>vulgaris</i> var. <i>altissima</i>	<i>Populus trichocarpa</i>	<i>Morus nigra</i>	<i>Morus alba</i>
					
Common names	Topinambur, Jerusalem artichoke, girasole	Sugar beet	Balm poplar	Black mulberry	White mulberry
Leaf attributes	Hairy, hispid thin ± wobbly	Hairless thin wobbly	Hairless rigid	Hairy thin	Hairless thin
Growth form	Herb	Rosette	Tree	Tree	Tree
Category	Experimental *	Control for topinambur*		Experimental *	Control for black mulberry*

See online version for color images

Huffman and his teams in their two leaf swallowing studies with captive chimpanzees (Huffman and Hirata 2004; Huffman *et al.* 2010), and black mulberry* (*Morus nigra*) as experimental plants. Control plants sugar beet (*Beta vulgaris* ssp. *vulgaris* var. *altissima*), balm poplar (*Populus trichocarpa*), and white mulberry (*Morus alba*) had leaf characteristics similar to those of the experimental plants but lacked a hairy leaf surface. We used two plant species as controls (sugar beet and balm poplar) to control for inter- and intraplant differences in topinambur*. Black mulberry* and white mulberry belong to the same genus and the morphological differences between these two species are not substantial. We used the keepers' judgment to decide whether the plants were novel, but it is theoretically possible that the apes had previously received plants similar to those that we used. One possible exception in terms of novelty was sugar beet because apes were already familiar with another variety of this species.

We collected the plants/branches in the Leipzig area (balm poplar) and Halle/Saale area (black mulberry*, white mulberry), or planted them especially for this study (topinambur*, sugar beet). We collected fresh plants or branches every morning before testing and placed them in water to maintain freshness. We removed old and broken leaves (all species), flowers (topinambur*), buds (balm poplar), beets (sugar beet), and fruits (black mulberry*, white mulberry) before testing. We rinsed the plants carefully with water to clean them. We provided subjects with full plants (topinambur*, sugar beet) or branches (balm poplar, black mulberry*, white mulberry) with a similar number of leaves.

Experimental Procedure

We conducted the study between August 8 and November 1, 2010. We provided subjects with the various plants and C. Menzel observed and videotaped the apes' behavior toward them in two different conditions: individual and social.

Individual Condition All 42 apes participated in this condition, which took place in the subjects' testing or sleeping room. We conducted these sessions in the morning, usually between 08:30 and 10:30 h. Before testing, the keepers gave the subjects their regular small breakfast of vegetables and fruit. Before a testing session started, the experimenter attached one plant to the mesh caging of the test cage with a burlap ribbon. We filmed the subject for 10 min after it voluntarily entered the testing cage, and then it was released into the enclosure. If the subject attempted to take plant material into the enclosure, the experimenter asked the subject for it. Once the ape had vacated the testing room the experimenter removed any remaining plant material. In the majority of cases we tested subjects individually and out of sight of others, except females with dependent offspring. We noted whether an individual could observe another subject. If more than one ape was in the testing cage, the experimenter filmed only the focal subject. The 5-yr-old female chimpanzee Kara, the 5-yr-old male chimpanzee Kofi, and the 2-yr-old female gorilla Zola (Table IV) were in the testing cages while their mothers were the focal subjects. After the end of the mothers' test we placed a new plant (same species) in the testing cage and let the offspring in while the mother stayed in an adjacent cage. The sliding door to this cage was half-open, so that only the offspring (now the focal subject) could get through. Coding began when the subject had at least half of its body through the door to the test cage.

We conducted tests with all five plant species (Table II). Each subject received only one plant per day. Subjects received topinambur*, balm poplar, and sugar beet, as one testing block, with at most a 1-d interval, and black mulberry* and white mulberry with at most a 1-d interval. Each block was separated by several days (mean=32.13±SD 23.62 d). Each subject ($N=42$) received two blocks of topinambur* – balm poplar – sugar beet (for exceptions and the exact testing course of each subject see Table IV). In addition, we provided 12 of the subjects with mulberries (black mulberry* and white mulberry) once (Table IV). Six chimpanzees (all from the big group) received the mulberries before they participated in the social condition and before they received the two blocks of topinambur* – balm poplar – sugar beet. Three bonobos received mulberries after their first block of topinambur* – balm poplar – sugar beet and two bonobos before. One gorilla participated in one mulberry block before he received two blocks of topinambur* – balm poplar – sugar beet. The order topinambur* – balm poplar – sugar beet was constant but we counterbalanced the starting plant (for black mulberry* – white mulberry as well) between subjects for age, sex, and rearing history for each testing block.

Social Condition Only chimpanzees (excepting Unyuro) participated in this condition, which took place in their enclosures while they were together with other group members, replicating the setup in Huffman and Hirata (2004) and Huffman *et al.* (2010). All tests took place between 12:00 and 13:30 h, immediately before the apes' noon meal. The experimenter threw a plant toward an ape from an observation tower. We recorded all interactions between the apes and the plants. If a plant was split into one or more pieces, we filmed leaf ingestion. In this setup, it was not possible to recover the plant remains. Filming continued for 20 min, longer if leaves were ingested, and never exceeded 1 h.

Testing of this social condition took place on 18 consecutive days in September 2010 with topinambur*, balm poplar, and sugar beet. We attempted to randomize the order of the plants and subjects that received them first but this was not always possible owing to the group setup (Table V). A group received only one plant per day. We conducted no experiments in the individual condition with these subjects at this time.

According to the testing schedule (Table IV), six subjects of the big and all six members of the small chimpanzee group were naïve to topinambur*, balm poplar, and sugar beet. The experimenter tried to give the plants to these six subjects. Consequently, each group received 18 plants on 18 days in a row.

Fecal Samples

If a subject ingested leaves without clearly chewing them, potentially indicating leaf swallowing, we attempted to inspect its feces. This was not always possible. Mostly, we could retrieve and inspect feces excreted during the night (see Results). Two of the authors (C. Menzel, A. Fowler) examined the collected feces for the presence of undigested folded leaves.

Data Analysis

We coded the recorded videos of the individual condition, second by second, for *leaf chewing* (including leaf eating) and *leaf swallowing*. We defined *definite leaf*

swallowing as the slow and deliberate ingestion of whole leaves, i.e., *complete leaf swallowing*, or parts of leaves, i.e., *partial leaf swallowing*, without chewing them. *Unclear leaf swallowing* is characterized by the slow and deliberate ingestion of leaves but we could not exclude chewing entirely. We indicate where we included these unclear cases in our analysis. If visible, we also coded whether the subject appeared to fold a leaf (part) inside the mouth (*leaf folding*). In addition, we scored *leaf inspection*, defined as touching a leaf carefully with the lips, and *other behaviors*, which were all direct interactions with the plant or parts of it, except carrying or holding it in the hand(s), e.g., eating stalks.

We coded videos of the social condition only for occurrences of *leaf swallowing* and when a subject observed a leaf swallowing conspecific closely (face oriented to and <1 m away from mouth of leaf swallowing ape).

An experienced field researcher (A. Fowler) further examined *leaf swallowing* events to confirm the first coder's (C. Menzel) assessment. Another independent observer coded 15 % of video clips (40/269 sessions of the individual condition and 6/36 of the social condition). We balanced these randomly selected sessions for ape and plant species. Because leaf swallowing was rare, we selected sessions containing it (*definite* and *unclear leaf swallowing*) preferably for reliability coding to introduce diversity. Interobserver reliability was good (individual condition: Cohen's $\kappa=0.691$; social condition: Cohen's $\kappa=0.652$).

For each subject we scored the percentage of sessions in which *leaf chewing* and *definite leaf swallowing* occurred as a function of plant species. We combined data from balm poplar and sugar beet (and controlled for the number of control plant sessions) to compare control plants (balm poplar and sugar beet) with topinambur*. We tested for differences in leaf swallowing frequency between plant species using the Wilcoxon signed-rank test. We also compared the duration of each behavior class as percentage of exact coding time for experimental and control plants using the Wilcoxon signed-rank test. We used Fisher's exact test to detect sex and infection effects. We tested for a relationship between age and leaf swallowing occurrence using a logistic regression, and for a correlation of age and interaction time with plants using a Spearman correlation. We used a Kruskal–Wallis test to test for species differences in general interaction time with topinambur* and inspection time of topinambur* leaves. All tests were two-tailed and conducted with SPSS 16.0.

We first present the main findings and then break them down by species for a more detailed analysis. Finally, we compare the species. The [Appendix](#) provides further information to testing schedule and results.

Results

Behavioral Observations

Eight of 24 chimpanzees and one of six bonobos displayed definite leaf swallowing behavior, which always occurred with the hairy plant topinambur* (Table III). Of these nine subjects, two female chimpanzees (Alexandra, Kara) and the male bonobo (Kuno) were naïve before they performed leaf swallowing. All other individuals may have observed others engaging in leaf swallowing in the social condition. Overall, in

Table III Overview of subjects which showed (definite and repeated unclear) leaf swallowing behavior

	Name	Species (group)	Plant	Condition (sessions)	LS experience	Fecal inspection
Definite leaf swallowing	Kara	Chimpanzee (big)	T*	SC (4/6)	Naïve	n. a.
			T*	IC (1/2)	Definite ^b	n. a.
	Lobo	Chimpanzee (big)	T*	SC (1/6)	Potential observation ^a	n. a.
			T*	IC (1/2)	Potential observation ^a	n. a.
	Pia	Chimpanzee (big)	T*	SC (2/6)	Potential observation ^a	n. a.
			T*	IC (2/2)	Potential observation ^a	n. a.
	Tai	Chimpanzee (big)	T*	SC (2/6)	Potential observation ^a	n. a.
	Alex	Chimpanzee (small)	T*	SC (1/6)	Potential observation ^a	n. a.
			T*	IC (1/2)	Potential observation ^a	Leaves
	Alexandra	Chimpanzee (small)	T*	SC (6/6)	Naïve	Leaves
			T*	IC (2/2)	Definite ^b	Leaves
	Fifi	Chimpanzee (small)	T*	IC (1/2)	Potential observation ^a	n. a.
	Jahaga	Chimpanzee (small)	T*	SC (1/6)	Potential observation ^a	No leaves
			T*	IC (2/2)	Potential observation ^a	Leaves
Kuno	Bonobo	T*	IC (2/3)	Naïve	Leaves	
Unclear leaf swallowing	Kofi	Chimpanzee (big)	T*	SC (1/6)	Potential observation ^a	n. a.
	Unyoro	Chimpanzee	T*	IC (2/2)	Naïve	No leaves
	Kuno	Bonobo	BM*	IC (1/1)	Definite ^b	n. a.
	Luiza	Bonobo	T*	IC (2/2)	Potential observation ^c	No leaves
	Ulindi	Bonobo	BM*	IC (1/1)	Naïve	No leaves
			T*	IC (1/2)	Potential observation ^c	No leaves

T* = topinambur* (hairy); BM* = black mulberry* (hairy); SC = social condition; IC = individual condition; LS = leaf swallowing; leaves = undigested leaves in at least one feces sample; no leaves = no undigested leaves in the feces; n. a. = feces not available

^a Could observe leaf swallowing in social condition

^b Performed definite leaf swallowing in previous session with topinambur*

^c Could observe Kuno swallowing leaves

the 12 sessions in which leaf swallowing occurred in the individual condition, we recorded 14 complete and 325 partial definite leaf swallowing events. In addition to the definite leaf swallowing cases, several more subjects showed unclear leaf swallowing with hairy plants (topinambur* or black mulberry*; Table III). These events involved neither definite chewing nor definite leaf swallowing. Typically, chewing was not clearly visible although the mouth moved. Folding also occurred in these cases. Two male chimpanzees (Kofi, Unyoro) and three bonobos (Kuno, Luiza, Ulindi; Table III) displayed this behavior repeatedly. These unclear leaf swallowing events never occurred with any of the hairless control plants (balm poplar, sugar beet, and white mulberry).

In the individual condition leaf swallowing subjects used a mean of $61.8 \pm \text{SD } 26.7$ % of available leaves for definite leaf swallowing and $72.0 \pm \text{SD } 27.2$ % for definite and unclear leaf swallowing.

Fecal Samples

In total, we inspected 23 fecal samples (Table VI). None were diarrheic. We found undigested folded leaves in 6 of 13 samples from subjects that showed definite leaf swallowing (Table VI). We collected most fecal samples the morning after testing (mean: 21.7 h later; range: 5–28 h; $N=23$). In one case in which we could determine the passage time of leaves it took 20–22 h (Table VI). Leaf swallowing subjects stayed at the location where feces were collected a mean of 11 h ($N=6$); thus passage time ranged 8–24 h. We inspected the feces of two chimpanzee subjects (Alexandra and Alex) that showed definite leaf swallowing on other days after they rejected or clearly chewed leaves (control samples). We did not find undigested leaves in any of these five control samples.

Chimpanzees

Eight chimpanzees showed leaf swallowing (Table III). Female Kara and male Lobo, as well as females Pia and Tai, first received topinambur*, balm poplar and sugar beet, or black mulberry* and white mulberry, respectively (Table IV) and showed no leaf swallowing in this individual condition. When tested later in the social condition, Kara swallowed leaves in the first session with topinambur*. Pia and Tai also started swallowing topinambur* leaves in this first session but without observing Kara closely. However, theoretically they could have observed Kara before and therefore should not be considered naïve to leaf swallowing. Lobo, who observed Tai and Pia closely swallowing leaves in the first two topinambur* sessions, started swallowing leaves in the third topinambur* session of the social condition. Females Sandra and Swela, as well as males Lome and Robert, observed leaf swallowsers closely in the social condition but never showed leaf swallowing behavior.

None of the chimpanzees in the small group had access to any of the testing plants before taking part in the social condition. Female Alexandra showed leaf swallowing in the first social session with topinambur*. Females Fifi, Annett, and Jahaga observed Alexandra closely in this first session. Jahaga also started swallowing leaves in this first session with topinambur*, and male Alex observed her. Later, Alex swallowed topinambur* leaves in the social condition. Fifi, who observed Alexandra closely several times, showed leaf swallowing in one of the following individual sessions. The topinambur* leaf ingestion of one female chimpanzee (Gertrudia) was characterized by some folding elements followed by clear chewing, except for two events when chewing was not clearly visible. This subject also observed leaf swallowsers closely during the social condition. Female Annett observed leaf swallowsers as well but never showed leaf swallowing.

Across both groups, four chimpanzee females (Alexandra, Kara, Pia, and Tai) showed leaf swallowing without closely observing a conspecific; six subjects (Robert, Lome, Sandra, Swela, Annett, and Gertrudia) closely observed a leaf swallower but never engaged in leaf swallowing; and four chimpanzees (Lobo, Fifi, Jahaga, and Alex) first closely observed a conspecific swallowing leaves and then showed the behavior later.

There was no sex difference in leaf swallowing occurrence (2/8 males, 6/16 females; Fisher's exact test: $P=0.667$). Parasite infection had no effect on leaf swallowing occurrence (4/18 parasite-infected, 4/6 parasite-free; Fisher's exact test: $P=0.129$). There was a negative relationship between leaf swallowing and age (logistic regression: Wald $\chi^2(1)=3.868$, Cox–Snell $R^2=0.285$, model $P=0.005$, $P=0.049$, $N=24$).

Individual Condition Seven chimpanzees showed definite leaf swallowing in the individual condition. Leaf swallowing occurred only with topinambur* and not with its control plants, balm poplar and sugar beet (Wilcoxon signed-ranks test: $T=28$, $P=0.016$, $N=7$), and, when including unclear leaf swallowing cases, it also occurred only with topinambur* and with none of its control plants, balm poplar and sugar beet ($T=45$, $P=0.004$, $N=9$). Folding occurred only with topinambur* and with none of its control plants, balm poplar and sugar beet ($T=55$, $P=0.002$, $N=10$). We did not observe definite or unclear leaf swallowing nor folding with black mulberry* or white mulberry. Subjects chewed the leaves of control plants—balm poplar and sugar beet—in more sessions than they chewed topinambur* leaves ($T=91$, $P=0.014$, $N=14$). However, chimpanzees spent the same amount of time chewing topinambur* and control leaves, balm poplar and sugar beet ($T=89$, $P=0.107$, $N=15$). The total interaction time with topinambur* and its controls—balm poplar and sugar beet—did not differ ($T=176$, $P=0.473$, $N=24$) and was also similar between black mulberry* and white mulberry ($T=14$, $P=0.563$, $N=6$). Chimpanzees spent more time inspecting topinambur* leaves with their lips than they did leaves of the control plants, balm poplar and sugar beet ($T=99$, $P=0.002$, $N=14$). The time spent interacting with topinambur* correlated negatively with age (Spearman correlation: $\sigma=-0.573$, $P=0.003$, $N=24$).

Social Condition Seven chimpanzees showed definite leaf swallowing in the social condition. We observed this behavior in all 12 (six big group- and six small group-) sessions with topinambur*. Male Kofi showed unclear leaf swallowing with topinambur*. Leaf swallowing occurred only with topinambur* and with none of its control plants, balm poplar and sugar beet (Wilcoxon signed-ranks test: $T=28$, $P=0.016$, $N=7$).

Bonobos

One naïve male bonobo (Kuno) swallowed topinambur* leaves without chewing them (definite leaf swallowing) in his first session. Females Ulindi and Luiza showed unclear leaf swallowing (with black mulberry* or topinambur*; Table III). Our sample size was too small to run meaningful statistical tests.

Gorillas

Female gorilla Viringika appeared to chew a topinambur* leaf on one occasion, but the chewing was not clearly visible and the ingestion was not slow and

deliberate, which is a criterion for leaf swallowing. Further, she chewed previous and subsequent leaves clearly. Therefore, we do not consider any of the gorillas to have shown either definite or unclear leaf swallowing. Gorillas showed the same duration of interaction in topinambur* and its control plants, balm poplar and sugar beet (Wilcoxon signed-ranks test: $T=12$, $P=0.844$, $N=6$). Only one male subject (Gorgo) received the mulberries, and he showed no interest (zero interactions) in these plants.

Orangutans

No orangutan showed definite or unclear leaf swallowing. Orangutans spent more time interacting with the control plants—balm poplar and sugar beet—than topinambur* (Wilcoxon signed-ranks test: $T=21$, $P=0.031$, $N=6$).

Species Comparisons

Chimpanzees, bonobos, gorillas, and orangutans spent a similar time interacting with topinambur* (Kruskal–Wallis test: $\chi^2=0.522$, $df=3$, $P=0.914$) and its controls, balm poplar and sugar beet ($\chi^2=5.045$, $df=3$, $P=0.169$) (Fig. 2). There were no species differences in duration of inspection of topinambur* leaves ($\chi^2=0.895$, $df=3$, $P=0.827$). We visualize the differences between the percentage of time spent on each behavior class separately for

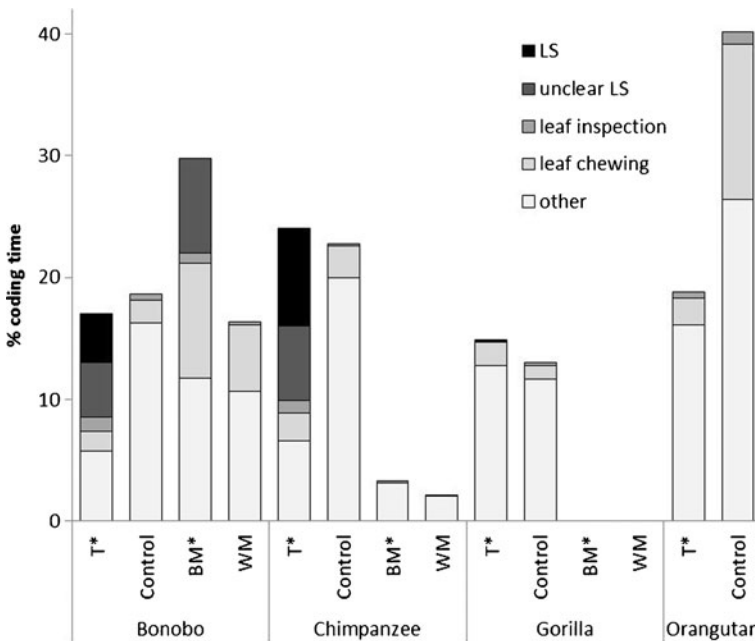


Fig. 2 Percent of total coding time for each coded behavior class separated by plant and ape species. T* = topinambur* (hairy); Control = balm poplar (hairless) and sugar beet (hairless); BM* = black mulberry* (hairy); WM = white mulberry (hairless); LS = leaf swallowing.

leaf-swallowers, unclear leaf-swallowers, and non-leaf-swallowers in Online Resource 1.

Discussion

Eight of 24 chimpanzees and one of six bonobos showed definite leaf swallowing behavior, later confirmed by fecal analyses, when processing rough-surfaced leaves but not when processing leaves with a smooth surface. Moreover, three of these apes displayed the behavior without having the opportunity to see another ape engaging in this behavior during the course of the study. In contrast, none of the gorillas or orangutans tested displayed leaf swallowing.

Our study confirmed the results of two previous studies reporting leaf swallowing in naïve healthy chimpanzees in the laboratory (Huffman and Hirata 2004; Huffman *et al.* 2010). In addition, it showed that some naïve bonobos also displayed this behavior in captivity. Thus, leaf swallowing in chimpanzees and bonobos may represent a latent solution (*sensu* Tennie *et al.* 2009) for processing rough-surfaced leaves rather than a behavior that must and can be acquired only by social learning. More precisely, a combination of genetic predisposition, individual learning, and plant affordances (roughness) can satisfactorily explain its independent emergence in multiple individuals. Nevertheless, social information may still play an important role in spreading this behavior within a group, at least with regard to its timing (Huffman *et al.* 2010). In the current study most of the subjects started swallowing leaves in the social condition, which is consistent with the view that they started once they observed the behavior. Nonimitative social learning mechanisms are the most likely mechanisms, e.g., contagion, stimulus enhancement, response facilitation (Whiten and Ham 1992; Whiten *et al.* 2004).

This is the third experimental study that has found leaf swallowing in captive great apes. Overall, across these three separate studies, leaf swallowing spontaneously appeared in six captive populations: one chimpanzee group and one separated individual in Huffman and Hirata (2004); two chimpanzee groups in Huffman *et al.* (2010); and two chimpanzee groups and one bonobo group in this study. Wild-born individuals may have acquired leaf swallowing in the wild via high-fidelity social learning and subsequently carried this behavior into zoo populations by social transmission. However, although this may explain the results of previous experiments in which the majority of chimpanzees were either wild-born or of unknown origin (Huffman and Hirata 2004; Huffman *et al.* 2010), it cannot explain our results because all but one ape included in our study were born in captivity. This, together with the occurrence of leaf swallowing in many independent wild populations—across several species—renders high-fidelity cultural transmission very unlikely as a necessity for acquisition of leaf swallowing in great apes, although we cannot definitively exclude this possibility.

Gorillas and orangutans did not display leaf swallowing behavior even though these species were as interested as chimpanzees and bonobos in topinambur*. One possible explanation for the absence of leaf swallowing in

our gorilla sample is simply that this behavior, although present, may be rare among gorillas and thus difficult to detect with our small sample size. Our orangutan sample was also small, so caution is needed, but the absence of leaf swallowing is consistent with observations in wild orangutans (van Schaik, *pers. comm.*). Owing to the small sample sizes we cannot draw strong conclusions about species differences regarding leaf swallowing.

We observed definite cases of leaf swallowing only with rough-surfaced leaves (topinambur*). We also recorded two unclear cases with black mulberry*, a plant whose leaves possess hairs but with a less rough surface than topinambur*. In addition, repeated folding, an indicator of an ingestion method different from normal eating, occurred only with topinambur* and black mulberry*. In contrast, subjects always chewed leaves of hairless control plants and never folded them before swallowing. This indicates a different response to hairy compared to hairless leaves. Our study thus supports the hypothesis that plant characteristics (hairiness/roughness) are important for initiating leaf swallowing behavior. As far as we know, the plants offered to the apes have no irritating chemicals, and the edges of the leaves were not sharp. Hence, if we assume that leaf swallowing aims to reduce gut transmission time (GTT; Huffman and Caton 2001), this would seem to be due solely to the physical features of the leaf surface. In our study, chimpanzees spent more time touching topinambur* leaves than leaves of hairless control plants with their lips. This may be to check the surface structure of a leaf. However, it may also provide a first impression of taste, and only a chemical analysis of compounds could exclude a chemical motivation. It is also possible that the effect of leaf swallowing is triggered jointly by physical and nonactive chemical properties of the leaves.

Another issue that should be addressed in future studies is the *degree of roughness* that elicits leaf swallowing. In our study, the male bonobo Kuno showed definite leaf swallowing with topinambur*. Later, when exposed to black mulberry*, which has a less rough surface, he showed unclear leaf swallowing. There may be a threshold of roughness for each individual from which point on leaf swallowing can be triggered. A future measurement for roughness, e.g., number, length, and thickness of hairs, might help to explore which plants are suitable for leaf swallowing.

Our results showed a negative correlation between leaf swallowing occurrence and age in chimpanzees. Because adult chimpanzees are conservative in their feeding patterns (Nishida *et al.* 1983), these observations indicate that leaf swallowing may appear at an early age, and social learning may help to increase the probability of its reoccurrence. This concurs with observations that young chimpanzees (Huffman and Wrangham 1994) and bonobos (A. Fowler, *pers. obs.*) explore rough leaves intensively when their mothers show leaf swallowing.

Both healthy chimpanzees and those with parasites engaged in leaf swallowing. Healthy subjects in previous experimental studies performed leaf swallowing (Huffman and Hirata 2004; Huffman *et al.* 2010). These results are in line with observations of apparently healthy wild apes, i.e., those displaying no signs of discomfort, swallowing leaves (chimpanzees: Boesch 1995; Wrangham and Goodall 1989; Wrangham and Nishida 1983; bonobos: Fowler and Fruth unpub. obs.).

It may be that apes perform this behavior prophylactically (Hart 2005). However, even if this hypothesis were correct, infected subjects should show more leaf swallowing compared to healthy conspecifics. If leaf swallowing reduces GTT (as described by Huffman and Caton 2001), then any benefit from a reduced GTT could explain the behavior. For example, in addition to removing parasites, a reduced GTT might be part of an optimal foraging behavior. A reduced GTT may help in efficiently harvesting nutrients at a time when they are particularly abundant and/or needed, as long as these particular nutrients require only some fraction of the normal GTT to be extracted. In this way, more such food could be processed in a given time interval, and more nutrients could be extracted. This effective-harvesting hypothesis could also explain the seasonality of leaf swallowing (chimpanzees: Huffman *et al.* 1997; Kawabata and Nishida 1991; bonobos: Dupain *et al.* 2002). All hypothesized explanations could, in theory, play some role, and our results cannot help to distinguish between them. All of our subjects received a continuous supply of high-quality food and showed no signs of deficiency. There was no obvious need or motivation for them to harvest rare or special nutrients and thus no apparent need to reduce GTT via leaf swallowing.

In the wild, apes perform leaf swallowing primarily in the early morning, sometimes even before their first food intake (Boesch 1995; Dupain *et al.* 2002; Wrangham and Goodall 1989; Wrangham and Nishida 1983). We tried to test the subjects as early as possible but all had received their morning meal before testing. It is possible that we would have found a higher rate of leaf swallowing if subjects had received the plants before their morning meal. However, timing does not seem to have a huge effect on the occurrence of leaf swallowing in captivity because existing studies have documented leaf swallowing even after food intake. The occurrence of leaf swallowing in captive apes at later times of the day is even more surprising because wild chimpanzees sometimes chew leaves of plants used for leaf swallowing when ingesting them in the afternoon or evening (Huffman and Wrangham 1994; Krief *et al.* 2006; Newton and Nishida 1990).

In conclusion, our findings support the hypothesis that leaf swallowing is a latent solution in *Pan*, which is expressed on encountering rough, but not smooth, surfaced leaves. We expect a similar mechanism for gorillas though none of six tested gorillas showed the behavior during the course of this study. The occurrence of this behavior, however, may be modulated by several factors including species, age, and social influences. Although our study shows that leaf swallowing can emerge spontaneously as a response to rough-surfaced plants, it also suggests that witnessing other individuals leaf swallowing may further promote its appearance.

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Appendix

Table IV List of subjects and their testing schedule

Species	Name	Session											
		1a	1b	1c	SC	2a	2b	2c	3a	3b	3c	4a	4b
Chimpanzee (<i>N</i> =24)	Corrie	B	S	T*	X	S	T*	B					
	Dorien+	S	T*	B	X	T*	B	S					
	Fraukje	S	T*	B	X	T*	B	S					
	Kara	S ^{a,b}	T ^{*a,b}	B ^{a,b}	X	T ^{*a,b}	B ^{a,b}	S ^{a,b}					
	Frodo	WM	BM*		X	T*	B	S	T*	B	S		
	Lobo	B	S	T*	X	S	T*	B					
	Lome	S	T*	B	X	S	T*	B					
	Natascha	T*	B	S	X	S	T*	B					
	Patrick	T*	B	S	X	B	S	T*					
	Pia	WM	BM*		X	B	S	T*	T*	B	S		
	Riet	WM	BM*		X	S	T*	B	B	S	T*		
	Robert	BM*	WM		X	B	S	T*	B	S	T*		
	Sandra	B	S	T*	X	T*	B	S					
	Swela	BM*	WM		X	T*	B	S	B	S	T*		
	Tai	BM*	WM		X	S	T*	B	B	S	T*		
	Ulla	T*	B	S	X	B	S	T*					
	Kofi	T ^{*a,b}	B ^{a,b}	S ^{a,b}	X	B ^{a,b}	S ^{a,b}	T ^{*a,b}					
	Alex				X	B	S	T*	S	T*	B		
	Alexandra				X	S	T*	B	T*	B	S		
	Annett				X	T*	B	S	T*	B	S		
	Fifi				X	T*	B	S	S	T*	B		
	Gertudia				X	S	T*	B	B	S	T*		
	Jahaga				X	B	S	T*	B	S	T*		
	Unyuro	S	T*	B		T*	B	S					
Bonobo (<i>N</i> =6)	Joey	WM	BM*			S	T*	B	T*	B	S		
	Kuno	T*	B	S		BM*	WM	T*	T*	B	S	B	S
	Limbuko	S	T*			BM*	WM						
	Ulindi+	BM*	WM			T*	B	S	S	T*	B		
	Luiza	BM ^{*a}	WM ^a			T ^{*a,b}	B ^a	S ^a	S ^a	T ^{*a,b}	B ^a		
	Yasa+	B	S	T*		WM	BM*		B	S	T*		
Gorilla (<i>N</i> =6)	Bebe	B	S	T*		T*	B	S					
	Gorgo	BM*	WM			B	S	T*	B	S	T*		
	Kibara	S	T*	B		B	S	T*					
	Louna	B	S	T*		T*	B	S					
	Viringika	T*	B	S		S	T*	B					
	Zola	T ^{*a,b}	B ^{a,b}	S ^{a,b}		S ^a	T ^{*a,b}	B ^a					
Orangutan (<i>N</i> =6)	Bimbo	B	S	T*		B	S	T*					
	Dokana+	B	S	T*		S	T*	B					

Table IV (continued)

Species	Name	Session											
		1a	1b	1c	SC	2a	2b	2c	3a	3b	3c	4a	4b
	Kila+	T*	B	S		B	S	T*					
	Padana+	T*	B	S		S	T*	B					
	Pini+	S	T*	B		T*	B	S					
	Raja	S	T*	B		T*	B	S					

f = female; m = male; age in years at the beginning of the study; T* = topinambur* B = balm poplar; S = sugar beet; WM = white mulberry; BM* = black mulberry*; session: 1, 2, 3, and 4 means test block over three (a, b, c) /two (a, b) consecutive days (individual condition); SC = social condition over 18 d; X = subject participated social condition; + mother was accompanied by an unweaned offspring (not listed) in the cage during testing

^a Individual was with mother (focal subject) in the same cage during testing

^b Second test, now offspring as focal subject (mother is one row above)

Table V Testing schedule for the social condition

Big chimpanzee group		Testing day	Small chimpanzee group	
Subject which received plant first	Plant		Subject which received plant first	Plant
Lome	T*	1	Fifi	B
Tai	B	2	Alex	T*
Frodo	S	3	Jahaga	S
Natascha	S	4	Fifi	T*
Pia	B	5	Gertrudia	B
Pia	T*	6	Jahaga	S
Lobo	B	7	Alexandra	T*
Swela	S	8	Alexandra	T*
Frodo	S	9	Alexandra	S
Tai	T*	10	Fifi	T*
Not determinable	S	11	Alexandra	B
Pia	B	12	Alexandra	T*
Lome	T*	13	Alexandra	B
Pia	S	14	Alexandra	S
Lobo	T*	15	Alexandra	B
Lobo	T*	16	Alexandra	S
Pia	B	17	Fifi	S
Tai	B	18	Alexandra	B

T* = topinambur; B = balm poplar; S = sugar beet

Table VI Overview of fecal samples

Name	Species	Sex	LS	Plant	Hours after testing	Duration of stay	Leaves present in sample
Alex	Chimpanzee	m	Yes	T*	22	12	Yes
			No	S	22	14	No
			No	T*	22	14	No
			No	B	22	14	No
Alexandra	Chimpanzee	f	Yes	T*	21	13	Yes
			Yes	T*	22	2	Yes
			Yes	T*	22	14	Yes
			Yes	T*	21	2	No
			Yes	T*	20	13	No
			Yes	T*	21	14	No
			Yes	T*	20	13	No
			No	B	22	14	No
			No	S	22	14	No
			Jahaga	Chimpanzee	f	Yes	T*
Yes	T*	21				2	No
Yes	T*	28				0	No
Kuno	Bonobo	m	Yes	T*	23.5	13	Yes
			Yes	T*	23	14	No
Luiza	Bonobo	f	Unclear	T*	24	0	No
Ulindi	Bonobo	f	Unclear	BM*	5	3	No
			Unclear	T*	24	0	No
Unyoro	Chimpanzee	m	Unclear	T*	24	2	No
			Unclear	T*	23.5	13	No

f = female; m = male; T* = topinambur*; B = balm poplar; S = sugar beet; BM* = black mulberry*; LS = leaf swallowing; time data in hours

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