Primates (2004) 45:113–118
DOI 10.1007/s10329-003-0065-5

ORIGINAL ARTICLE

Michael A. Huffman · Satoshi Hirata

An experimental study of leaf swallowing in captive chimpanzees: insights into the origin of a self-medicative behavior and the role of social learning

Received: 8 August 2002 / Accepted: 17 October 2003 / Published online: 23 January 2004

Abstract Chimpanzees in the wild swallow the rough hispid leaves of certain plant species as a means of physically expelling intestinal parasites. A plant with such a leaf texture was introduced in 36 trial sessions to a captive group of 11 healthy adult chimpanzees to investigate the possible origin and acquisition of leaf swallowing behavior. One male (housed separately from the group during testing) and one female, both captive born, spontaneously exhibited the behavior on their first trial without prior opportunity to observe others with this plant. Six other chimpanzees on their first trial displayed a phobic response to these leaves and rejected them entirely, while another two chewed and swallowed the leaves in a normal way. Four individuals eventually exhibited the behavior, after having approached and closely observed the leaf swallowing of the first female to exhibit the behavior in the group. Four of the six individuals that initially avoided the leaves never overcame their phobia toward this plant and were not in proximity to a chimpanzee performing leaf swallowing during test sessions. Individuals born to wild chimpanzee mothers were no more likely to perform the behavior than captive-reared group mates. These results suggest that the acquisition of this behavior is based in part on a propensity to fold and swallow rough, hispid leaves, but that the acquisition and spread of leaf swallowing within a group is likely to be socially influenced. This study provides support for the hypothesis that leaf swallowing originated in the wild from opportunistic feeding behavior and was later passed down in the form of a self-medicative behavioral tradition.

Keywords Feeding · Social tolerance · Behavioral tradition · Self-medication

Electronic Supplementary Material Supplementary material is available in the online version of this article at http://dx.doi.org/10.1007/s10329-003-0065-5

M. A. Huffman (✉)
Primate Research Institute, Kyoto University,
41-2 Kanrin, Inuyama, Aichi 484-8506, Japan
E-mail: huffman@pri.kyoto-u.ac.jp

S. Hirata
Great Ape Research Institute,
Hayashibara Biochemical Laboratories, Inc., Okayama, Japan

Introduction

Attention was first brought to leaf swallowing behavior by Wrangham and Nishida (1983) when they pointed out the significance of this ingestive behavior as unlikely to be that of providing any nutritional value. They noticed a pattern for the occurrence of folded, undigested leaves of *Aspilia* species in the dung of chimpanzees at both Gombe and Mahale. Currently, leaf swallowing is documented in the greatest detail in chimpanzees at four study sites in East Africa (Mahale, Gombe, Kibale, and Budongo), where its use is associated with the expulsion of adult intestinal nematodes and or cestode proglottids (Wrangham 1995; Huffman et al. 1996; Huffman and Caton 2001). Leaf swallowing has since been noted to occur in at least 22 social groups of chimpanzees, bonobos, and lowland gorillas at 13 study sites across Africa (Huffman 2001). The 34 different plant species selected at these sites vary in life form (herb, vine, shrub, and tree), but they all share the common property of being rough and hispid (Huffman 1997).

The widespread occurrence of leaf swallowing and this universal criterion for selecting rough, bristly leaves suggests a behavioral predisposition for leaf swallowing in all African great apes. There is also evidence to suggest that transmission within the group occurs at least in part by some form of social learning (Huffman and Hirata 2003). Observations from the wild suggest that individuals' first exposure to leaf swallowing and other forms of self-medicative behavior occurs at an early age, not when ill themselves, but by observing the behavior of close family members or associates that are ill.

Chimpanzees as young as 1 year of age closely watch this behavior and have been seen to attempt immediately thereafter to perform it on their own with varied success, regardless of health condition (Huffman and Seifu 1989; Huffman and Wrangham 1994). At this stage, it is most likely treated as one more element of the mother's foraging repertoire that engages the infant's interest.

We do not expect that the behavior is first acquired because of any understanding of its self-medicative function, rather, that the self-medicative aspects of use are likely to be learned over time if the appropriate selective forces (e.g. parasite infection) are present in the habitat in question. A combination of learning the context of use from watching others and positive feedback from any perceived personal relief from physical discomfort that leaf swallowing may assist in providing the ingestor is predicted to occur. Presently, the details of this underlying mechanism and how long it takes to acquire the behavior in its self-medicative context is unclear. It is extremely difficult to collect such evidence from the field given that these traditions appear to be already well established in all groups where leaf swallowing is known to occur (Huffman 2001). Furthermore, as the behavior itself occurs at low frequencies in the wild due to strong seasonality linked with periods of parasite reinfection (Huffman et al. 1996; Huffman 1997), the acquisition process of the behavior by new individuals is difficult to follow precisely under natural conditions.

There is a range of possibilities for how leaf swallowing behavior started and how individuals come to swallow leaves instead of simply chewing them. At one extreme, animals may have an innate tendency to select appropriate properties in plants when ill, so that the role of social context is local enhancement. That is, naive individuals may have their attention drawn to areas with plant species used by others (Huffman and Wrangham 1994). At the other extreme, animals may have a propensity to swallow certain items without chewing, but due to unfamiliarity with rough bristly leaves in their daily diet, must somehow learn that such leaves can be ingested before they are able to learn about any possible benefit from doing so. Thus, initial acquisition by young or naive individuals, like the proposed origin of this behavior itself, may occur in the context of opportunistic feeding behavior that is later molded over time through further individual experience and association of its practice with illness in other group members. To elucidate some of these important questions regarding the intrinsic nature and acquisition process of leaf swallowing behavior, we conducted a study on a socially living group of captive chimpanzees.

Methods

The study was conducted between 9 October and 11 November 1997 on a group of 11 (3 males, 8 females) adult chimpanzees used in cognitive studies at Kyoto University's Primate Research Institute in Inuyama, Japan (Table 1). Among the 6 individuals born in Africa, all but 2 of the oldest (Gon, Puchi) were brought into captivity and reared from the age of 1 year. The remaining 5 individuals were captive born and or human reared in Japan or Europe. The veterinary staff routinely examines the chimpanzees. None of the subjects displayed symptoms of parasite infection during the study period.

From 1996 up to the time this study was conducted in 1997, the chimpanzees had daily access to an environmentally enriched outdoor enclosure containing 63 species (390 individual plants) of trees and shrubs, a flowing stream, and an 8-m-high multi-tiered tower (Ochiai and Matsuzawa 1998, 1999). Prior to the experiments described below, their exposure to plants in the outdoor compound was limited to these 63 known species and a few local grass species that spontaneously took root. None of the plants in the compound resembled the texture of plants used for leaf swallowing by chimpanzees in the wild.

The test plant species used in this study, *Helianthus tuberosus* (Compositae), was selected because the leaves are virtually identical in texture to species such as *Aspilia mossambicensis, Lippia plicata,* and *Ficus exasperata* used by chimpanzees at Mahale, Gombe, and elsewhere. No member of the study group had been exposed to this or other species resembling it in leaf texture prior to testing. *H. tuberosus* grows semi-wild between June and November along roadsides, in open lots, and in some gardens in the neighborhood of the Institute. Fresh branches were collected within 20 min prior to testing and placed in water to maintain their freshness. Native to North America, *H. tuberosus* is a nontoxic plant whose leaf and stem are often used as cattle fodder. Introduced to Japan over 100 years ago, the tubers are a delicacy consumed by people in some rural areas of the country. The plant is known as ''kiku imo'' in Japanese and ''earth apple'' in English.

In total, 36 trial sessions were conducted on the chimpanzee colony, with a minimum of 3 sessions per individual. A branch of 29–40 cm in length with 18–40 leaves and occasionally 1–8 flowers was given to an individual, selected randomly over the study period. It was possible to call an individual chimpanzee to the wall of the enclosure and drop a branch down to it from the observation

Table 1 Leaf swallowing test subjects at the Primate Research Institute (*PRI*)

Name	Sex	Age[a]	Arrived at PRI (age at arrival)	Origin (date of birth)
Gon	M	31	30.1.79 (12)	West Africa, pet in Japan (1966, month unknown)
Puchi	F	31	30.1.79 (12)	West Africa, pet in Japan (1966, month unknown)
Reiko	F	31	3.7.68 (1.6)	West Africa (December 1966)
Mari	F	21	30.1.78 (1.5)	West Africa (June 1976)
Akira	M	21	30.1.78 (1.5)	West Africa (June 1976)
Ai	F	21	10.11.77 (1)	West Africa (October 1976)
Pendesa	F	20	12.11.79 (2.7)	Japan Monkey Centre (2 February 1977)
Chloe	F	16	28.1.85 (5)	Paris Zoo (13 December 1980)
Popo	F	15		PRI[b] (7 March 1982) daughter of Puchi–Gon
Reo	M	15		PRI[b] (18 May 1982) son of Reiko–Gon
Pan	F	13		PRI[b] (7 December 1983) daughter of Puchi–Gon

[a] Age at the time of experiments in October 1997
[b] Artificial insemination, hand reared

point. Normally tests were conducted on individuals in a social group setting in the outdoor enclosure ($n = 28$) with all or most members present. Three test sessions, however, were conducted with a sub-group of 3 individuals in a smaller holding room; one plant was introduced and the 3 interacted consecutively with the same plant. During the entire study period, adult male Reo was kept in a separate enclosure from the main group during the day, with occasional access to his mother or other female companions. During testing Reo was always alone in all 3 of his trial sessions. Due to the physical separation of his enclosure from the main outdoor enclosure, Reo had no opportunity to see other individuals during their sessions and vice versa. The old adult male Gon and adult female Pan were also tested alone on one occasion each. None of the subjects had access to the test plant species outside of these trial sessions.

Observations were recorded by the authors using 8-mm video and by handwritten notes. All feeding behaviors and behavioral interactions between the focal animal and others in the group were recorded. To obtain complete behavioral sequences of a subject's response to the plant material and interactions with others, observations were continued for 5 min after the focal individual no longer possessed test plant material. There was no stealing or disruption by others while the plant was in the possession of the focal subject. Because it was impossible to retrieve a plant from the enclosure if it was abandoned or retrieved by another, the behavior of the new possessor and interactions with all others was recorded as a new trial session. In eight cases, an onlooker picked up all of the remaining plant material after the original focal subject freely discarded it. Because of this, no plant material was left in the enclosure after the end of the final trial session of any given day.

To independently verify our assessment of leaf swallowing in the trial sessions, individuals were separated from the rest of the group when they were brought inside for the night and put singly into a night sleeping room when day-to-day management and ongoing research protocol allowed. The following morning, after these individuals were rejoined with the group, feces in their sleeping rooms were inspected.

Results

Verification of leaf swallowing behavior

Folding and swallowing of leaves became the major mode of ingestion for 6 of the 11 individuals at some point during the study (Fig. 1). The behavior was similar to that observed for chimpanzees in the wild (LS-Wild ESM1, LS-Chloe ESM2), supporting the notion of a species-wide propensity to perform this behavior in chimpanzees. Leaves were deliberately folded, using a combination of lips, palate, and tongue, while a leaf still attached to the stalk was slowly drawn into the mouth. The behavior was distinct from normal feeding as chewing action was overtly absent and the leaves were deliberately put into the mouth one at a time. Of those 6 individuals that leaf swallowed, there was no significant difference in the number of African born (3/6) versus captive born (3/5) subjects (Fisher's exact test, two-tailed, $P = 1.000$, NS) to exhibit this behavior.

Results of the 11 next-morning follow-up dung inspections are presented in Table 2. All individuals selected for the follow-up inspections were observed

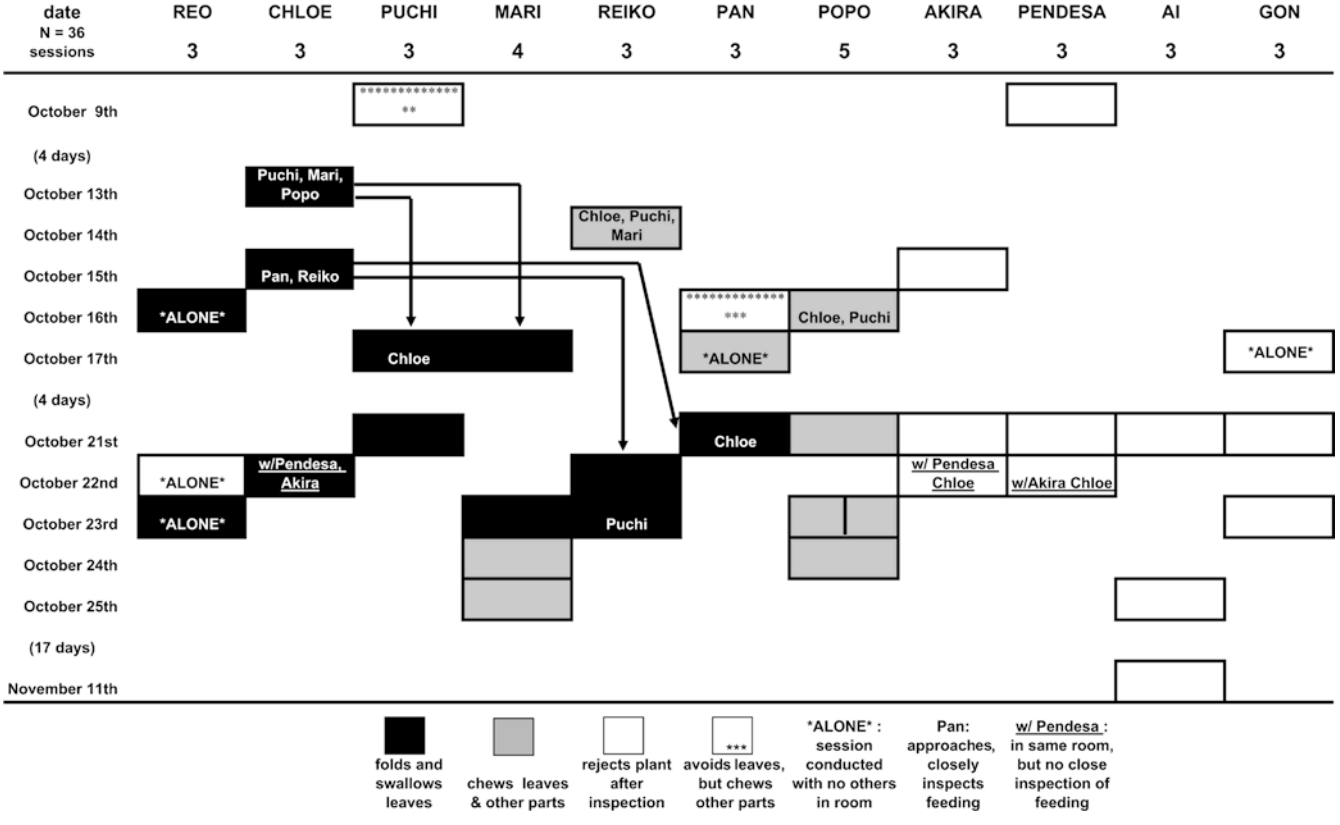

Fig. 1 Observed responses of chimpanzees in trial sessions with novel plant stimuli (*Helianthus tuberoses* L.). *Solid lines* connecting boxes denote putative social learning network between Chloe (leaf swallowing "demonstrator") and individuals that first displayed leaf swallowing behavior in subsequent trial sessions

Table 2 Results of dung inspection the day after individual observation sessions. *Underlined subjects* were observed to swallow leaves during the trial session

Date	Subject	Parts ingested the previous day	Contents of dung
10 October	Puchi	Stalk, flowers	No leaf trace
14 October	Chloe	Leaves, flowers	3 folded leaves
15 October	Reiko	Leaves, flowers	No leaf trace
16 October	Chloe	Leaves, flowers	10 leaves
18 October	Puchi	Stalk, leaves, flowers	2 leaf fragments
18 October	Mari	Flowers, leaves	No trace
22 October	Pan	Stalk, leaves	1 leaf
22 October	Puchi	Stalk bark, leaves, flowers	No leaf trace
23 October	Reiko	Stalk bark, leaves, flowers	6 leaves
24 October	Mari	Stalk, leaves	No leaf trace
24 October	Reiko	Stalk, leaves	6 leaves

to have ingested some or all parts of the plant during the test session in question. Eight of these cases were of individuals directly observed to exhibit leaf-swallowing-like behavior during the session. The following morning, in 6 of these 8 cases, dung was found to contain one to six folded, nondigested *H. tuberosus* leaves. No whole or partial undigested leaves were found in the 3 cases in which individuals were only observed to chew leaves and or other plant parts.

Individuals' first response to rough hispid leaves

The first response to the leaves varied from individual to individual. Chloe and Reo, two captive-born individuals, spontaneously displayed leaf-swallowing-like behavior in their first session without the benefit of observing it in other group members. Chloe consistently displayed this pattern as her major mode of ingestion during all three of her test sessions. Mari also folded and swallowed a portion of the leaves on the branch given to her on her first (and second) session. She did so after having closely observed Chloe fold and swallow leaves 4 days earlier (Fig. 1).

The typical first response to the plant for six other individuals was an almost phobic rejection of the rough hispid leaves (Akira, Pendesa, Ai, Gon, Puchi, and Pan). Four of these individuals consistently rejected the entire plant throughout the study, while the other two discarded all of the leaves but ate other plant parts (Pan, Puchi). In contrast, two other individuals, (Reiko and Popo) chewed and ate the leaves in their first trial session. Popo continued to chew and eat leaves in all of her subsequent sessions. She displayed no aversion whatsoever, rapidly consuming everything (Fig. 1).

Leaf swallowing and social interactions among individuals during the trial session

Leaf swallowing was observed in 10 of the 31 trial sessions conducted in a group setting. Individuals in possession of *H. tuberosus* attracted the attention of others in 5 of these sessions (Fig. 1). Puchi, Mari, Reiko, Pan, and Popo approached within close proximity (< 1 m) to, and intently inspected, Chloe while she exhibited leaf swallowing during her 1st and 2nd trial sessions. This group of females also approached and closely inspected one another when leaves and other parts were being eaten (Fig. 1), showing their mutually tolerant social relationships. With the exception of Popo, these females all subsequently exhibited leaf swallowing behavior themselves for the first time 2–9 days after having observed Chloe perform leaf swallowing behavior. During this study, Chloe was the first and only possible model of leaf swallowing for these four females (Fig. 1). Chloe approached closely and intently watched the first instance of leaf swallowing exhibited by Reiko and Pan.

Due to other ongoing research Ai and Pendesa were frequently absent when group-setting test sessions were conducted in the outdoor enclosures. During ten sessions outdoors in which leaf swallowing was observed, Ai was absent during seven and Pendesa during six sessions. Akira, Gon, Ai, and Pendesa were never observed to approach and inspect the feeding behavior of others in the possession of *H. tuberosus*, whether they were leaf swallowing or chewing leaves or other parts of the plant. These four individuals consistently rejected *H. tuberosus* in all of their test sessions.

Discussion

Possible modes of acquisition and the origin of leaf swallowing

This is the first ever attempt to investigate leaf swallowing under semi-controlled conditions. Bearing in mind the limited sample size and management restraints on observational procedure, some basic aspects of the nature of leaf swallowing and insights into the possible modes of acquisition of this behavior by chimpanzees can be considered. The spontaneous performance of leaf swallowing by two individuals during their first trial, in the absence of a leaf swallowing "demonstrator," shows that chimpanzees may have a propensity to fold and swallow rough hispid leaves. This supports evidence from the wild that the behavior can emerge without inter-group social contact in geographically isolated populations or subspecies (sec. Huffman and Hirata 2003). However, unlike their counterparts in the wild that often exhibit this behavior when ill and/or infected with

parasites (Wrangham 1995; Huffman et al. 1996), these captive individuals were parasite free and showed no visible signs of ill health when they performed the behavior. From this we conclude that folding and swallowing of leaves is not an innate response to parasite infection. Indeed, the initial response for more than half of the subjects was a phobic avoidance of these leaves or the entire plant. Our results support the current hypothesis regarding the origin of leaf swallowing behavior (Huffman and Wrangham 1994), which proposes it may have originated in the feeding context of a novel plant item. It is suggested here that the leaf's rough hispid texture encourages the peculiar mode of ingestion, that is, folding and swallowing leaves whole.

Our results also support observations in the wild that the acquisition and spread of leaf swallowing within a group is at least in part socially influenced, rather than being solely the product of individual trial-and-error learning. It is clear that the behavior was not acquired by every individual in this study via the same mode of learning. Excluding Chloe and Reo, who seemingly acquired leaf swallowing behavior spontaneously, the other individuals that later exhibited the behavior may indeed have used multiple modes of learning over the period of acquisition (sec. Visalberghi and Fragaszy 1990). Among the individuals that eventually exhibited the behavior during our study, social tolerance among them in the feeding context (sec. van Schaik et al. 1999) is considered to have been an important facilitator of exposure to leaf swallowing, and thus opportunities for social learning. As suggested for object manipulation in Japanese macaques (Huffman and Quiatt 1986) and foraging-related tool-use acquisition in orangutans (van Schaik 2003), here too, interpersonal social networks and social tolerance could be important factors in the transmission of leaf swallowing behavior. This is further supported by the fact that those individuals that never approached and observed another chimpanzee leaf swallowing never overcame their phobia of the plant's rough, hispid leaves. All individuals that eventually exhibited leaf swallowing behavior did so only after having seen the behavior being exhibited by Chloe, the first individual in the social group observed to display folding and swallowing of *H. tuberosus* leaves spontaneously.

Future studies

Controlled studies of self-medicative behavior in parasitized organisms are rare and limited to mice (Vitazkova et al. 2001) and invertebrates (Karban and English-Loeb 1997). There are obvious ethical reasons why we chose not to conduct a controlled study on chimpanzees in the context of parasite infection. We have shown here that there are important things to be learned without such invasive methods. Given the fact that bonobos and lowland gorillas too are known to habitually exhibit leaf swallowing behavior in the wild (Huffman 1997), the propensity for folding and swallowing of rough hispid leaves is expected to be a shared trait of all African great apes. It follows then that the self-medicative function of leaf swallowing behavior must be a secondary adaptation of a feeding response brought about by leaf texture, raising the question as to how the self-medicative context of leaf swallowing emerged independently across Africa.

Further refined, noninvasive testing of captive chimpanzee groups naive to rough hispid leaves is being planned. Similar controlled and noninvasive studies regarding the acquisition process of leaf swallowing and other self-medication in the African great apes and other primates is strongly encouraged. Greater attention should be paid to the social networks of group individuals to grasp greater detail of the possible mode(s) of social learning involved in the transmission of such behaviors within the group (e.g. White and Burgman 1990; Ginsberg and Young 1992; Coussi-Korbel and Fragaszy 1995; Whitehead 1997). Such studies are expected to increase our understanding of the possible origins of self-medicative behaviors and the role social learning may play in their maintenance in nature.

Acknowledgements We wish to give our sincere thanks to Testuro Matsuzawa, Professor of the Section of Language and Intelligence (PRI) and Professor Iver Iversen of Northern Florida State University, for their encouragement and support in conducting this study. We are indebted to the primate health care staff of the Center for Human Evolution Modeling Research for their assistance and day-to-day care of the chimpanzees. The present research was partially financed by Grants 07102010, 12301006, and 10CE2005 from the Ministry of Education, Science, Sports, and Culture, Japan. We thank our anonymous referees and Jean-Baptiste Leca for their insightful comments and criticisms of the manuscript in its final stages. Last but not least, we thank the chimpanzees for their patience and cooperation, without which this study would not have been possible.

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