Coprophagy in wild bonobos (*Pan paniscus*) at Wamba in the Democratic Republic of the Congo: a possibly adaptive strategy?

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Abstract Four cases of coprophagy and two cases of fecal inspection were identified during the 1,142 h of observing wild bonobos at Wamba in the Luo Scientific Reserve in the Democratic Republic of the Congo. At least 5 females in the study group practiced coprophagy and/or fecal inspection. According to our daily behavioral observations, boredom and stress, insufficient roughage, and the search for essential nutrients could not explain the coprophagy. Several episodes observed in this study indicated that bonobos might have sought and ingested certain valuable food items, such as hard *Dialium* seeds, in feces during relatively lean seasons. Although coprophagy occurred only rarely among wild bonobos, this practice appeared to represent a possibly adaptive feeding strategy during periods of food scarcity rather than a behavioral abnormality.

Keywords Bonobo, *Pan paniscus*, Coprophagy, Inspect feces, Adaptive strategy, Wamba.

Introduction

Coprophagy refers to the ingestion of one's own (autocoprophagy) or others' (allocoprophagy) fecal material; this practice occurs in wild populations of lagomorphs, rodents, and, to a lesser degree, piglets, foals, dogs, and primates (Soave and Brand 1991; Fish et al. 2007). African apes, gorillas, and chimpanzees practice coprophagy both in captivity and in their natural environments (Harcourt and Stewart 1978; Akers and Schildkraut 1985; Goodall 1986; Hook et al. 2002). Although coprophagy in wild chimpanzees has been seen only rarely, this practice has been observed in several long-term study sites, including those in Gombe, Mahale, Assirik, Fongoli, and Semliki (Nishida et al. 1999; Payne et al. 2008).

Although the cause of coprophagy in chimpanzees and gorillas remains unclear, several hypotheses have been proposed. (1) Boredom and stress: In captivity, fewer social stimuli and less time to search for food can cause boredom and stress. Such situations might induce coprophagy or other abnormal behaviors (Akers and Schildkraut 1985; Nash et al. 1999). It has been hypothesized that coprophagy among wild mountain gorillas might be associated with periods of heavy rain because gorillas might need to relieve boredom and/or eat something warm under these circumstances (Harcourt and Stewart 1978). (2) Insufficient roughage: Deficiencies in sources of dietary roughage (e.g., fibrous leaves) can occur in captivity and might increase the frequency of coprophagy (Fritz et al. 1992). (3) Essential nutrients: In some lagomorphs and rodents, coprophagy is apparently an adaptive trait permitting full digestion of complex carbohydrates. It also provide vitamins, minerals, amino acids, and other nutrients (Soave and Brand 1991). Vitamin B12 might be a key reason for engaging in coprophagy among primarily herbivorous apes because it is present only in animal matter (Oxnard 1966). (4) Food scarcity: Chimpanzees at Gombe in Tanzania engaged in coprophagy during the 1981 dry season, a period of fruit scarcity (Goodall 1986). The pressures of foraging in food-scarce environments might induce coprophagy. (5) Reingesting valuable food items such as meat and hard seeds: Hard seeds such as *Dialium* spp. and *Saba comorensis* might represent the target in the reingested feces; that is, coprophagy might constitute a potentially efficient way of ingesting the nutritional content of seeds that have already passed through the stomach (Uehara 1979; Goodall 1986; Krief et al. 2004; Payne et al. 2008).

Although coprophagy has been observed among wild bonobos (*Pan paniscus*) at Wamba and Lomako (ethogram created in a workshop, “Behavior, Ecology and Conservation of Wild Bonobos: Current Activities and Plans for the Future,” Inuyama, Japan, 2003), this is the first report to include details about coprophagy among wild

bonobos. I examined the applicability of the aforementioned hypotheses to my observations.

Methods

I studied bonobos in the E1 group at Wamba (0˚11’8”N, 22˚37’58”E) in the northern sector of the Luo Reserve in the Democratic Republic of the Congo. All individuals in the group were identified and well habituated. Artificial provisioning was abolished in 1996. The history of the E1 group and the details of the study site have been described by Kano (1992), Furuichi et al. (1998), Hashimoto et al. (2008) and Idani et al. (2008).

Observations were made during three study periods. Period 1: August 11–November 2, 2007; Period 2: January 31–March 11, 2008; Period 3: September 1, 2008–January 4, 2009. I attempted to locate the E1 group during 6 days of each week and to follow the parties from one sleeping site to the next. I recorded *ad libitum* the behaviors of those bonobos within sight as I followed them. Total observation time was 1,141 h 57 min across 156 days (Table 1). The E1 group was comprised of 23–26 individuals including 9 adult males and 6–7 adult females (15 years or older) during the period under investigation.

In this study, coprophagy refers to feces-eating behavior, irrespective of whether bonobos ate the feces or extracted and ate something selectively, or object of ingestion was not confirmed.

Results

I observed four episodes of autocoprophagy (cases 1–4) and two episodes of fecal inspection (cases[a] 1 and 2) (Table 1). Coprophagy occurred 0.35 times per 100 hours.

Four females (2 adults, 1 subadult, and 1 immature bonobo) engaged autocoprophagy. During the episodes of fecal inspection, 2 adult females (one of whom, Sala, practiced coprophagy as well) defecated directly into their own hands, placed the feces close to their faces, and then dropped it without ingesting.

Cases 1 and 2 occurred in October, a month of high fruit availability, including fruits of *Landolphia* spp. (Apocynaceae), a favorite of bonobos. On the other hand, cases 3 and 4 occurred in December, a month in which fruit was relatively less plentiful (Kano and Mulavwa 1984; Mulavwa et al. 2008). When cases 3 and 4 occurred, most individuals in the E1 group showed symptoms of a flu-like disease (i.e., coughing, sneezing, and/or nose-picking) (Sakamaki et al. 2009). During this period of time, the E1 group members divided into relatively small parties and did not travel long distances each day. They ate a relatively restricted diet, which consisted primarily of fruits of *Dialium pachyphyllum*, *Dialium zenkeri* (Caesalpiniaceae), and *Musanga cecropioides* (Moraceae).

All feeding behaviors involved in coprophagy occurred high in the trees, rendering it difficult to observe the behavioral patterns in detail. However, case 4 of coprophagy was clearly observed; in this instance, Fuku, a subadult female, confidently used her lips to extract *Dialium* seeds from the feces in her hand, ate the seeds, and discarded other fibrous parts in the feces. In case[a] 2 and Case 4, bonobos held their feces in their hands to inspect and/or consume it. After dropping the feces, they rubbed their hands on the stems of a tree/vine. I did not see diarrheic individuals inspect and/or eat their feces, and most feces involved in the episodes seemed to be hard.

Discussion

This is the first report on the details of coprophagy among wild bonobos. This study indicated that bonobos only rarely engaged in coprophagy in natural environments. Although we cannot infer the cause of coprophagy on the basis of the data collected in this study, we can rule out certain previous causal hypotheses. Hypothesis 1, boredom and stress: We observed the subjects in their natural habitat, which involved searching for foods and interacting with group members. This environment was no less socially stimulating than is captivity. In addition, boredom during heavy rains could not explain the coprophagy observed in this study because coprophagy occurred outside of the months with the greatest rainfall (September-November; Mulavwa et al. 2008). Being followed by human observers almost all day might have been stressful to the bonobos. However, the bonobos in the E1 group were so accustomed to humans that they did not seem to be unduly stressed by being followed by the observers. Hypothesis 2, lack of dietary roughage: This hypothesis could not explain the coprophagy observed in this study because sources of roughage were almost always available in the habitat; for example, piths/shoots of terrestrial herb vegetation [e.g., *Aframomum* spp. (Zingiberaceae), *Haumania Liebrechtsiana* and *Megaphrynium macrostachyum* (Marantaceae)] and young leaves [e.g., *Scorodophloeus zenkeri* (Caesalpiniaceae)] were observed (Kano and Mulavwa 1984). Hypothesis 3, essential nutrients: Bonobos in the study group were able to consume essential nutrients such as Vitamin B12 by eating insect larvae, earthworms, vertebrates, and eggs of birds (Kano and Mulavwa 1984). Even if certain nutrients were derived from feces, the concentration of these nutrients in the feces would be insufficient for daily requirements. Further studies are needed to investigate nutrients in foods and feces.

The other hypotheses suggest variables that might have induced coprophagy among the bonobos in this study. Hypothesis 4, food scarcity: Contrary to expectation of this hypothesis, coprophagy observed in cases 1 and 2 occurred when favorite fruit

144 foods were relatively abundant. However, coprophagy in cases 3 and 4 occurred when
145 fruit was less plentiful and when the bonobos were traveling only a short distance, and
146 therefore, feeding activities were largely limited due to the epidemic of a flu-like
147 disease. Hypothesis 5, reingesting valuable food items such as hard seeds: Rogers et al.
148 (1998) reported that wild gorillas extract and consume *Dialium* seeds from feces, and
149 Krief et al. (2004) also reported that chimpanzees rehabilitated into a natural
150 environment ingested *Dialium* seeds extracted from feces. Certain hard seeds in feces,
151 such as *Dialium* spp., might be items of interest for gorillas and chimpanzees because
152 of their protein content (Krief et al. 2004; Payne et al. 2008). During the season that
153 included coprophagy, cases 1 and 2 and fecal inspection cases[a] 1 and 2, bonobos
154 primarily ate fruits of the *Landolphia* spp., the seeds of which are similar to those of
155 *Saba comorensis* that chimpanzees crunch and eat (Uehara 1979; Payne et al. 2008).
156 During the season including cases 3 and 4, bonobos primarily ate fruits of *Dialium* spp.,
157 and a bonobo was observed to extract the seeds in case 4. In case[a] 2 and case 4,
158 bonobos rubbed their hands on the stems of a tree/vine probably to clearn their hands
159 after they dropped the feces. These observations suggested that bonobos searched for
160 certain valuable food items in their feces during relatively lean food seasons.
161
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Table 1. Observations of coprophagy

Month and Year	Observation		Observation of coprophagy		
	No. days	Time			
Period 1					
August 2007	10	61 h 57 min	None	-	-
September 2007	21	137 h 9 min	None	-	-
October 2007	22	157 h 10 min	Case 1 (Oct 31)	Sala (adult female)	At 0921 h, she took her feces in her left hand and ate it. She again took her feces in her left hand and ate it. The feces seemed to be dark in color and hard.
November 2007	2	13 h 10 min	None	-	-
Period 2					
January 2008	1	10 h 58 min	None	-	-
February 2008	17	119 h 47 min	None	-	-
March 2008	7	66 h 58 min	None	-	-
Period 3					
September 2008	22	151 h 7 min	Case[a] 1 (Sep 24)	Sala (adult female)	At 0821 h, she evacuated a small amount of feces, which fell on the ground. She held the fecal material that emerged second in her left hand, moved it close to her face, looked at it carefully, and then dropped it.
October 2008	19	148 h 6 min	Case[a] 2 (Oct 10)	Hoshi (adult female)	At 1003 h, she held her feces in her right hand after appearing to experience some difficulty with the excretory process, moved it close to her face and looked at it, and then dropped it. Next, she rubbed her right hand on a woody vine.
			Case 2 (Oct 10)	Jacky (adult female)	At 1439 h, her feces fell between her fingers even though she positioned her hand close to her anus. She held the second feces in her left hand, moved it close to her face, looked at it, and then ate it.
November 2008	8	59 h 16 min	None	-	-
December 2008	25	211 h 43 min	Case 3 (Dec 5)	Nachi (2-year-old female)	At 0620 h, she grasped her feces in her right hand and ate it. The feces were about 5 cm long and seemed to be light in color.
			Case 4 (Dec 10)	Fuku (approximately 10-year-old female)	At 0731 h, she grasped her feces in her left hand. At 0732 h, she moved it close to her face and looked at it. At 0735 h, she ate it and dropped something that resembled seeds from her mouth. At 0736 h, she rubbed the palm of her left hand on a tree trunk. At 0741 h, she kept the feces in her hand while crunching seeds in her mouth. She used her lips to select only seeds from the feces, and chewed them in her mouth. She dropped other fibers or material from the feces. At 0747 h, she finished eating the feces and rubbed her left hand on a tree trunk. The feces seemed to be ocherous in color.
January 2009	2	4 h 36 min	None	-	-
Total	156	1141 h 57 min			