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ORIGINAL ARTICLE

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On the possible adaptive value of coprophagy in free-ranging chimpanzees

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Abstract Coprophagy occurred during major periods of feeding on fruits of *Dialium* spp. (Caesalpiniaceae) in a group of orphaned chimpanzees released in Conkouati Douli National Park, Republic of Congo. Since stress, boredom or food scarcity could not explain coprophagy according to our daily behavioral and veterinary control observations, we suggest that *Dialium* seeds were the item of interest in the feces. Two types of *Dialium* seeds were commonly found in the feces after chimpanzees swallowed the mesocarp and whole seeds together. These seeds were either whole and hard or whole/broken and soft imbibed. A mechanical and/or chemical effect of the gut passage may enable the chimpanzees to chew and ingest the seeds, thus providing nutritional intake.

Keywords Coprophagy · *Pan troglodytes troglodytes* · *Dialium* spp. · Feeding behavior

Introduction

Apes indulge in coprophagy in their natural environment as well as in captivity, even though this behavior seems to be more widespread among captive animals. Captivity can produce behavioral peculiarities such as stereotypical motor patterns or coprophagy, a problem particularly difficult to deal with in zoos.

Several hypotheses have been proposed to explain such behavior. In captivity, food deficiency may initiate coprophagic behavior (Hill 1966; Erwin and Deni 1979; Akers and Schildkraut 1985). Particularly, insufficient dietary roughage may compel chimpanzees (Fritz et al. 1992) and gorillas (Hladik 1978) to chew their feces to reproduce the natural behavior of making wadges. Among wild chimpanzees, periods of food scarcity may also induce coprophagy, as observed at Gombe, Tanzania, during the 1981 dry season (Goodall 1986). Among wild mountain gorillas, coprophagy may be correlated with periods of heavy rain when foraging activities are reduced: this behavior may result from boredom and a need to eat something warm (Fossey and Harcourt 1976; Harcourt and Stewart 1978; Hladik 1978; Akers and Schildkraut 1985).

Boredom and stress are often involved in explaining coprophagy among captive apes (Maple 1979; Hoff et al. 1994). In zoos, providing environmental enrichment, social stimuli, increasing the number and roughage content of meals, and more time to search for food should reduce such stereotypical behavior sometimes associated with regurgitation and reingestion (Akers and Schildkraut 1985).

Coprophagy may also reflect medical problems: it occurs in wild chimpanzees when feces are diarrheic and contain undigested parts of food (Goodall 1986).

Coprophagy can be adaptive, allowing the upkeep of ciliates that digest cellulose (Collet et al. 1984) and the assimilation of the vitamins synthesized in the hindgut, which are absorbed only in the foregut (Oxnard 1966; Hladik 1981). Caecotrophy, which is a peculiar type of coprophagy, greatly increases the nutrient intake of *Lepilemur*, a folivorous prosimian which thrives on the poorest diet observed among primates (Hladik 1978).

The observations presented in this paper concern a group of six chimpanzees (*Pan troglodytes troglodytes*) released in the wild since November 1996 by the HELP (Habitat Ecologique et Liberté des Primates) project in the Republic of Congo, in order to reinforce the wild population. All of them developed coprophagic behavior during the period of feeding on *Dialium* fruits, suggesting a peculiar use of reingested seeds.

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Methods

Study site

Data were collected on the Triangle site in Conkouati Douli National Park, 180 km north of Pointe-Noire, Republic of Congo. The study area covers 20.5 km^2 of tropical rain forest. Mean annual rainfall is 1,200 mm, mean annual temperatures vary from 24 to 26°C (Doumengue 1992). The river barriers surrounding the forest of the release site allow chimpanzees to habituate to the new environment, free from human interference. However, the rivers have tree bridges allowing encounters between wild and released chimpanzees (Tutin, unpublished data). Before the release, wild chimpanzee density in the Triangle was about 0.25 ± 0.07 km^2 and the density of herbaceous plants such as *Palisota barteri* (Commelinaceae) and *Aframomum* sp. (Zingiberaceae) was the same as in Kibale, Uganda, where chimpanzee density varies from 2.5 to 3.8 animals/km^2 (Tutin, unpublished data). Human activities are now excluded from the Triangle site in order to reduce the risks of extinction from hunting and other disturbance, as recommended by The World Conservation Union (IUCN) guidelines for reintroductions (Stanley-Price 1989, 1991; Beck et al. 1994; Kleiman et al. 1994, IUCN 1995). Access is allowed only to researchers and field assistants. Swamps cover 28.7% of the area, primary forest 19.5%, mangrove 17.8%, raphia swamps 15.7%, seasonally flooded forest 15.1% and Marantaceae forest, secondary forest and plantations occupy the remaining 3.2% of the area (Tutin, unpublished data).

Subjects

The six chimpanzees released in the Triangle were confiscated as a result of actions against illegal bush meat trade. They were seized by the Congolese authorities and entrusted to HELP (Habitat Ecologique et Liberté des Primates). Most of them were kept in captivity only very briefly. They were placed under semi-wild conditions in social groups on three islands in the Conkouati lagoon where they were fed fresh fruit and a milk drink with cereal twice a day. Veterinary (Ancrenaz, unpublished data; Ancrenaz et al. 1998) and feasibility studies (Tutin, unpublished data) were conducted before release. Five females and one male, from 6 to 10 years old, were released in the Triangle. They spent a few months to 6 years in captivity before being seized and released, first on the island and then in the Triangle where they were completely independent of humans (no food supplementation was given).

Data collection

Daily observations lasted from December 1996 to July 1997 while the reintroduction was being monitored. Released chimpanzees were habituated to human observers, but contact between chimpanzees and humans was avoided. Telemetric collars worn by four of the six chimpanzees helped observers to locate them. We used the scan-sampling method. The behavior, height and location of each individual and the weather were recorded every 10 min. Ad libitum focal sampling observations were made for unusual behavior, especially coprophagy, measured in terms of the number of feeding bouts. Diet was specified: the part and the species ingested, when identified, were recorded. Otherwise the item was collected, photographed, sketched and stored for future identification.

Daily veterinary observations and state of health estimations using non-invasive methods were practiced. Reproductive, digestive, respiratory and urinary functions, and stoutness were evaluated visually. If lesions or symptoms were diagnosed, veterinary examination including palpation was conducted. In any case, such detailed examinations were systematically conducted on a monthly basis. Seventy-seven fecal samples from identified chimpanzee were collected. Consistency and color were evaluated. A small part of the feces was kept for parasitological analysis by direct microscope observation and the remainder was washed in a sieve (1-mm mesh). The contents were listed; the large seeds were counted and the small seeds and non-fruit plant parts (fibers of leaves and stems, bark, insects) were rated for abundance on a scale from 0 to + + +. A phenological survey was carried out once a month on transects totaling 5 km.

Results

Observations on dietary adaptation

From December 1996 to July 1997, 16 animal species and 72 plant species corresponding to 90 food items were consumed (Didier-Krief 1998; Poullet, unpublished data). Time allocated to feeding activities varied between 47% to 72%, according to seasonal variation. Food diversity and abundance were regular throughout the study period, following food availability shown by phenological records (Didier-Krief 1998). During the survey, *Irvingia grandifolia* and *Irvingia gabonensis* (Irvingiaceae), some *Landolphia* spp. (Apocynaceae), *Grewia coriacae* (Tiliaceae), palm nuts (*Elaeis guineensis,* Arecaceae), and *Vitex doniana* (Verbenaceae) were the most common fruits eaten (Fig. 1). When the consumption of *Dialium* increased—between the 13th and the 22nd week—the other major fruits, *Landolphia* and *Irvingia*, were not present in the diet of the chimpanzees and vegetative parts were most often eaten.

Coprophagy

Chimpanzees ingested their own feces immediately after defecating in their hand. Some of them consumed all the feces, whereas others sorted out and picked only some seeds from the dung. This behavior occurred at any time during the day and was not related to any particular activity. We observed 1,973 bouts of coprophagy, with individual variation ranging from 214 to 504 across the six observed subjects (mean number for five females: 294; for the male: 504). Occurrence of coprophagy varied across the study period with a strong relation to *Dialium* intake (Spearman $r = 0.92$, $P < 0.001$, $n = 26$) (Fig. 2).

The intake of *Irvingia* (Spearman $r = -0.44$, $P = 0.024$, $n = 26$) has a weak negative correlation with coprophagy. *Landolphia* spp. (Apocynaceae) (Spearman $r = -0.29$, $P = 0.14$, $n = 26$) and vegetative parts of other plants, such as leaves, bark and stems (Spearman $r = 0.07$, $P = 0.72$, $n = 26$) consumed during the same period are not correlated with coprophagy. Chimpanzees in the Triangle site may consume at least six species of *Dialium* fruits (Caesalpiniaceae): *D. bipedensis, D. densiflorum, D. dinklagei, D. gossweileri, D. pachyphyllum, D. tesmanii*. They split the capsule and swallow the mesocarp and the seed together.

Analysis of fecal samples shows two types of *Dialium* spp. seeds. Some of them are hard, similar to those from ripe fruits, and others are soft, nacreous and imbibed whole or broken.

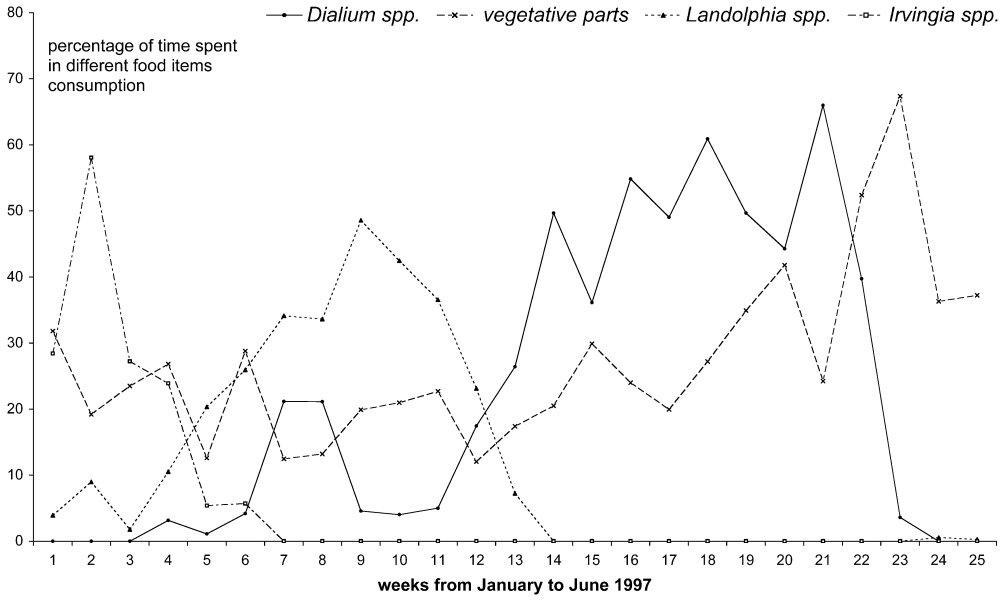

Fig. 1 Consumption of major food items (vegetative parts include stems, leaves, piths and bark of various species) by reintroduced chimpanzees from January to June 1997, the Triangle, Conkouati Douli National Park, Republic of Congo

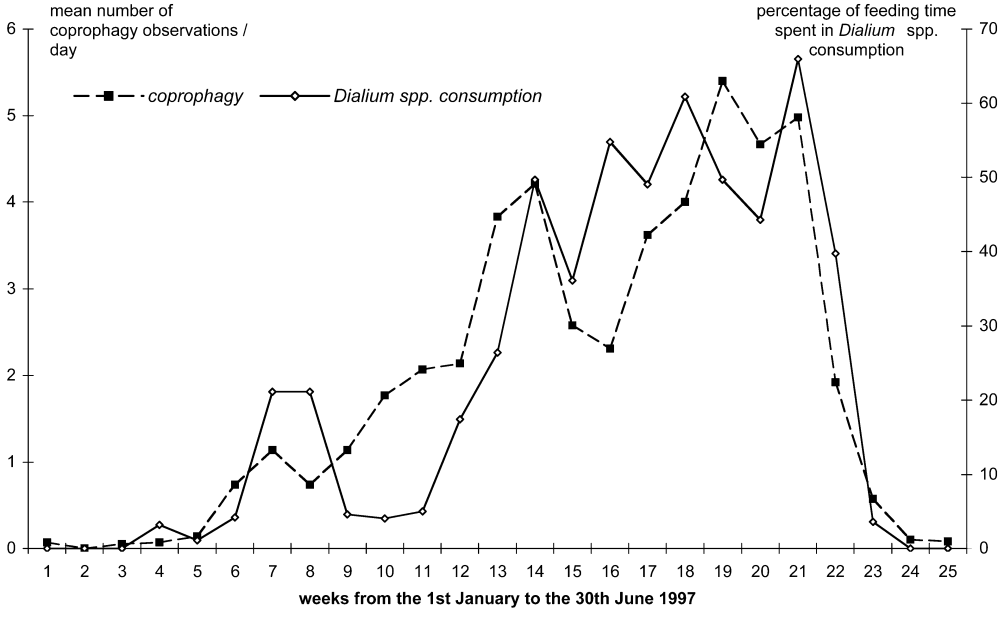

Fig. 2 *Dialium* spp. consumption and coprophagy in a group of reintroduced chimpanzees from January to June 1997, the Triangle, Republic of Congo

Similar observations have also been recorded in a wild individual in the Triangle. S.K. observed a large wild male chimpanzee, carrying his dung in his mouth on 13 April 1997. Seeing the observer, he was surprised, crossed the transect and the dung fell to the ground. The feces were washed and we observed the two types of *Dialium* spp. seeds; whole seeds of the hard type and softened crunched seeds of the soft type.

Health status

According to daily veterinary observations, released individuals were healthy during the study period. The body condition of the individuals was good and monthly veterinary examinations, including palpation, showed that none of the chimpanzees lost a significant amount of weight. Only 13 from 77 stool samples tested positive for intestinal parasites and the parasite load was not higher than that of wild chimpanzees (Krief et al. 2003).

Discussion

The correlation between the seasonality of *Dialium* and coprophagy rate suggests the hypothesis that, in the observed cases, coprophagy is a dietary, rather than stress-related behavior. The following five hypotheses previously proposed to explain coprophagy may be excluded from this survey:

1. Concerning food scarcity, the diet of rehabilitated chimpanzees was highly diverse during the 8-month study period and no apparent body weight loss was observed. Eating of insects was common and hunting was observed. Food availability in the Triangle was high (Tutin, unpublished data) and regular, according to phenology, during the survey. The mean proportion of time spent foraging and feeding (between 47% and 72% of daily activity at the Triangle) was quite similar to that observed in the wild chimpanzees of Gombe (46.5% to 60.2% after Wrangham 1977, and 35% to 67% after Goodall 1986).
2. Insufficient roughage was also excluded, since consumption of shoots, stems and leaves allowed the chimpanzees to express natural behavior such as wadge making.
3. Boredom or stress, often mentioned as determining coprophagy in zoos, was certainly not involved, since reintroduced chimpanzees exhibited complex tool use such as using leaves as sponges for blood or water, twigs for ant fishing and honey dipping, revealing that they had a rich and stimulating environment (Didier-Krief 1998).
4. No relationship of coprophagy with the weather and especially with rainfall has been noted, since the period with most coprophagy bouts covers both rainy season (including sunny days) and the beginning of the dry season.
5. Finally, coprophagy may be nutritionally important. For gorillas, which are known to be largely herbivorous, coprophagy may provide vitamin B_{12}, present in all animal matter but not in plant matter (Oxnard 1966). Reintroduced chimpanzees, however, consumed insects and vertebrates.

Our observations show that *Dialium* seeds may be the item of interest in the feces. In the context of feeding on a specific food item, observations of wild individuals strengthen our hypothesis. The observation of a wild adult chimpanzee in the Triangle and data from La Lopé, Gabon, confirm that wild chimpanzees and gorillas indulge in coprophagy during the fructification of *Dialium* spp. Hard *Dialium* seeds, crunched soft seeds and rolled testas from soft seeds were found in 2, 8 and 34% of gorilla dung samples, respectively (Voisey 1995; Tutin, personal communication). Tutin (personal communication) observed a similar correlation between consumption of baobab seeds (*Adansonia digitata*) and coprophagy. In February 2001, in the Kanyawara chimpanzees' community, S.K. observed an adult female (LP) carefully removing unidentified seeds from fresh elephant dung for 6 min, then crunching and swallowing them. LP was observed rummaging through another elephant dung 10 min later. Free-ranging provisioned Japanese macaques also removed undigested wheat grains and soybeans from feces to eat (Huffman, personal communication). In Mahale, Uehara (1979) reported cases of a female eating her feces, which were filled with the large seeds of *Saba florida* (Apocynaceae), and crunching them. Typically, the seeds are passed whole, but on occasion are chewed when immature or as in the cases observed by Uehara, when alternative food sources are scarce (Uehara, personal communication)

Nishihara (1995) described seed cracking as a foraging behavior peculiar to western lowland gorillas and a potentially efficient way of ingesting protein and/or fat. *Dialium* seeds collected at La Lopé, Gabon, contain 18.4% dry matter as crude protein (Rogers et al. 1990), the highest protein content in seeds eaten by gorillas at La Lopé (mean crude protein in seeds = 10.6, range = 4.1–18.4). *Dialium* seeds also present a high condensed tannin content (11.4%); although passing through the gut may not precipitate tannins inside the unbroken seeds, chimpanzees do tolerate fruits with such a high tannin content (Wrangham and Waterman, 1983).

We suggest that after the first passage of seeds through the gut, the hard seeds of ripe fruits have been softened. The efficiency of softening seeds after passing through the digestive tract has recently been discussed by Magliocca et al. (2003) as a mechanism of increasing nutritional supplement for consumers. Seeds present in the feces of chimpanzees that were swollen and nacreous could be either hard seeds that had been digested twice, or soft immature seeds. Chimpanzees were specifically looking for such seeds in their feces and often crunched them. In contrast, when they ate ripe fruit, they swallowed and never crunched the seeds. Coprophagy remains a puzzling behavior. Further observations in wild conspecifics must be undertaken to provide further data to confirm that it may be a way to make use of unavailable resources and to increase nutrient intake.

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