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BRIEF REPORT

Coprophagy by Wild Ring-Tailed Lemurs (*Lemur catta*) in Human-Disturbed Locations Adjacent to the Beza Mahafaly Special Reserve, Madagascar

KRISTA D. FISH[1]*, MICHELLE L. SAUTHER[1], JAMES E. LOUDON[1], AND FRANK P. CUOZZO[2]
[1]*Department of Anthropology, University of Colorado, Boulder, Colorado*
[2]*Department of Anthropology, University of North Dakota, Grand Forks, North Dakota*

Coprophagy occurs in a number of animal species, including nonhuman primates. During the 2003–2004 dry seasons at the Beza Mahafaly Special Reserve, Madagascar, we observed wild ring-tailed lemurs (*Lemur catta*) consuming dried fecal matter from three different species. Ring-tailed lemurs consumed human feces on 12 occasions, cattle feces twice, and feral dog feces once. Coprophagy in this population may be a behavioral adaptation that provides animals access to energy and nutrients and may be an important nutritional source for older, and/or dentally impaired individuals during the dry season. Am. J. Primatol. 69:713–718, 2007.

Key words: coprophagy; ring-tailed lemurs; habitat fragmentation; human–nonhuman primate interactions

INTRODUCTION

Coprophagy has been reported in a variety of mammal species including rabbits, rodents, dogs, horses, swine, nonhuman primates, and humans [Flurer & Zucker, 1988; Graczyk & Cranfield, 2003; Krysl et al., 1984; Soave & Brand, 1991]. Coprophagy refers to the consumption of fecal material. Animals may engage in autocoprophagy in which they feed on their own feces, or they may perform allocoprophagy and consume the excrement of another individual [Soave & Brand, 1991]. For lagomorphs and rodents, a particular type of autocoprophagy—caecotrophy—allows these animals to recycle nutrients and subsist on a low-quality diet despite their small body size [Pei et al., 2001; Soave & Brand, 1991]. In swine and horses, coprophagy supplies vitamins and nutrients to young offspring [Soave & Brand, 1991]. Most instances of reported coprophagy among nonhuman primates occur in captivity, where coprophagy may be an aberrant behavior associated with the stresses of confinement [Hook et al., 2002; Soave & Brand, 1991].

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*Correspondence to: Krista D. Fish, Department of Anthropology, Hale Science/CB 233, University of Colorado, Boulder, CO 80301. E-mail: Krista.Fish@Colorado.edu

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Coprophagy has also been observed in wild primates and is hypothesized to increase nutritional benefits. Wild mountain gorillas (*Gorilla beringei*) in the Virunga volcano chain and the Bwindi Impenetrable Forest engage in coprophagy [Graczyk & Cranfield, 2003]. Coprophagy in folivorous mountain gorillas likely supplies protein and inoculates the large intestine with symbionts that facilitate the digestion of plant materials [Graczyk & Cranfield, 2003]. Lowland gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*) consume feces during the fruiting season of *Dialium* sp. [Krief et al., 2004; Rogers et al., 1998]. Initial passage through the digestive system may soften the hard seeds of *Dialium* and reingestion of seeds via coprophagy may provide access to the protein-rich seeds [Krief et al., 2004]. Coprophagy has been observed in strepsirhine primates as well. Like rodents and lagomorphs, *Lepilemur leucopus* may ingest its own feces as a strategy to maximize protein intake given its low-quality folivorous diet [Hladik, 1979]. Allocoprophagy has also been described in *Eulemur* sp. [Overdorff, 1993].

Reports of interspecific coprophagy are common for invertebrates, but rarely observed in vertebrates [Frankenberg & Smith, 1967; Howden & Young, 1981; Robertson, 1982; Young, 1981]. Interspecific coprophagy may be an important source of energy or vitamins for some vertebrates. Cave salamanders (*Eurycea spelaea*) feed on the calorie- and vitamin-rich feces of gray bats (*Myotis grisescens*), whereas Egyptian vultures (*Neophron percnopterus*) eat carotenoid-rich ungulate feces, which supply them with the necessary vitamins to support their colorful pigmentation [Fenolio et al., 2006; Negro et al., 2002]. The white-winged crossbill (*Loxia leucoptera*) consumes the feces of river otters (*Lontra canadensis*) to gain calcium from the fish bones present in the feces or as an alternative food source during winter months [Gallant, 2004]. Here, we report incidences of wild ring-tailed lemurs (*Lemur catta*) consuming the fecal matter of three other species and discuss the possible adaptive role that coprophagy plays in the lives of older and/or dentally impaired individuals and ring-tailed lemurs in changing environments.

METHODS

The research was conducted at the Beza Mahafaly Special Reserve in southwestern Madagascar (23° 39′S, 44° 37′E). The reserve encompasses 80 ha of gallery forest, which is protected from domestic livestock by a fence along the perimeter. Adjacent to the southern boundary of the reserve is a field station that includes campsites for researchers, housing for reserve staff, a well, and other reserve buildings. At the time of this research, the camp contained two latrines: one pit latrine used by researchers and a traditional Mahafaly latrine used by the Mahafaly reserve staff and their families. According to local Mahafaly tradition, human waste is not put into the ground [Muehlenbein et al., 2003]. As a result, an above ground area of approximately 20 m^2 near the camp was used as a latrine. The fenced reserve and researchers' camp is surrounded by forest disturbed by the grazing of cattle, sheep, and goats.

The study was conducted during the May–October dry season when food availability is reduced [Sauther, 1993]. From June 17, 2003 to July 16, 2003, 39.5 h of behavioral data were collected on two groups of ring-tailed lemurs. One group of ring-tailed lemurs, Orange group, sleeps and forages inside of the reserve, but also exploits resources in and around the researchers' camp. Another group, Black group, lives in degraded forest adjacent to the reserve and also utilizes the camp area. We conducted 15-min scan samples on Orange and Black

groups in both the reserve and camp habitats. All occurrences of fecal consumption by lemurs were recorded ad libitum. These instances of fecal consumption by one or more group members feeding on a common source of feces were termed ''bouts.''

From June 13, 2004 to July 25, 2004, behavioral data collection was expanded to five groups: Orange, Black, Yellow, Teal, and Blue. Fifty hours of behavioral data were collected in 2004. Behavioral data were collected on Orange, Black, and Yellow groups while they were in reserve and camp habitats. Teal and Blue groups were not observed in the camp, but behavioral data collection for these groups was conducted in the reserve. As in 2003, behavioral data collection consisted of 15-min scan samples and ad libitum collection of coprophagous behaviors.

RESULTS

During 2003, we observed three bouts of coprophagy on human feces by individuals in Orange group. Consumption of human feces occurred in the latrine area utilized by the local Mahafaly staff and their families. Prior to the coprophagous behaviors, this ring-tailed lemur group was present in the researchers' camp and fed on discarded human food in the camp before moving to the latrine. Upon entering the latrine, lemurs fed or rested on the ground while a few individuals fed or rested in trees. Lemurs on the ground foraged among piles of human feces and selected only dry feces. After choosing a piece, the lemurs began licking and eating the feces. Feces were often discarded before the entire piece was consumed. The average duration of a feeding bout per group in the latrine was 23 min (SD = 8.3, $n = 3$). Of the 11 adult members of Orange group an average of five individuals per bout (SD = 2.7, $n = 3$) fed on human feces. Coprophagy was observed only among the members of Orange group in 2003 (Table I). However, a male from Yellow group was present on the periphery of Orange group during one period of fecal consumption, but did not consume any feces.

TABLE I. Bout duration and number of individuals engaged in human fecal consumption bouts during 2003 and 2004

Group bout	Year	Group (number of adults in group)	Bout duration per group (min)	Number of individuals engaged in human fecal consumption per minute during bout	
				Range	Mean
1	2003	Orange (11)	26	1–8	4.3 (SD = 1.86, $n = 26$)
2	2003	Orange (11)	14	2–10	6 (SD = 3.63, $n = 14$)
3	2003	Orange (11)	30	1–10	5.9 (SD = 3.63, $n = 30$)
4	2004	Orange (11)	3	1–3	2.3 (SD = 2.3, $n = 3$)
5	2004	Yellow (12)	4	1–5	1.5 (SD = 1.3, $n = 4$)
6	2004	Yellow (12)	11	1	1
7	2004	Yellow (12)	13	1–4	2.2 (SD = .99, $n = 13$)
8	2004	Yellow (12)	17	1	1
9	2004	Yellow (12)	3	1	1
10	2004	Yellow (12)	10	3	3 (SD = 0, $n = 10$)
11	2004	Yellow (12)	38	2–4	3.89 (SD = .45, $n = 38$)
12	2004	Black (9)	11	1–3	1.81 (SD = .98, $n = 11$)

In 2004, Yellow group had the highest frequency of coprophagy. Yellow group individuals consumed human feces eight times while Orange group individuals ate human feces once. Feeding bout duration per group was an average of 12.2 min (SD = 10.8, $n = 9$). The mean number of individuals in Yellow and Orange groups participating in feces consumption was 2.7 (SD = 1.4, $n = 9$). In addition to the consumption of human feces, individuals in Black group were observed eating the feces of zebu cattle twice and feral dogs once. Ingestion of zebu feces was focused on undigested vegetable matter. This behavior was initiated by an old female who was then joined by her younger daughters. On both occasions, the old female ate dried vegetation in conjunction with the zebu feces. Information regarding individual levels of coprophagy was collected in 2004. The individuals who exhibited the highest frequency of coprophagy were a male of Yellow group who had well-worn teeth with 56% tooth loss and a male of Orange group with 81% tooth loss [Cuozzo & Sauther, 2006].

DISCUSSION

Although coprophagy is found among many species of primates, it often occurs under conditions of captivity and frequently involves the ingestion of one's own feces or the feces of conspecifics. However, members of three groups of ring-tailed lemurs at Beza Mahafaly consume the feces of at least three other mammal species. What factors may explain the coprophagy observed in lemurs at Beza Mahafaly? Other species of wild primates consume their own feces to obtain nutrients that are accessible only after passage through the digestive tract. Animals that practice interspecific coprophagy also obtain energy and vitamins by ingesting fecal matter. The lemurs at Beza Mahafaly may obtain nutritional benefits from the feces that they consume. However, unlike most vertebrates that practice interspecific coprophagy, ring-tailed lemurs do not focus on fecal matter from one species. Instead, they consume feces from animals with a wide range of dietary strategies: an omnivore, a ruminant, and a carnivore. Because they are generalists in their pattern of feces consumption, it is unlikely that they are eating feces to obtain a specific vitamin. If ring-tailed lemurs are not feeding on feces to obtain specific nutrients, they may be doing so because this provides an easily accessible form of energy. At Beza Mahafaly, many individuals who engaged in this behavior were older lemurs with well-worn and/or missing teeth. The female who first ingested zebu feces was among the oldest of identified females (12 years old) and had over 36% tooth loss. Older and/or dentally impaired ring-tailed lemurs may consume the feces of other animals because it allows them access to nutrients that they are unable to obtain from harder food items such as tamarind fruit, which is an important dry season food for lemurs at this site. Health analyses of these individuals conducted during the study period suggested good health status in older individuals in coprophagous groups despite tooth loss [Cuozzo & Sauther, 2004]. Future research analyzing the nutritional composition of feces eaten by ring-tailed lemurs and exploring variation in food selection between different age groups of ring-tailed lemurs is needed to more adequately address these hypotheses.

Evaluating the adaptive value of coprophagy is an important goal. It appears that coprophagy is a local tradition not engaged in by all lemurs. Ring-tailed lemurs that do not range into the researcher's camp have not been observed practicing coprophagy. Ring-tailed lemurs are often considered to be a weed species as they occupy a variety of habitat types, quickly recover population

numbers following severe droughts, and can rapidly increase their population numbers when their diet is supplemented by humans [Gould et al., 1999; Jolly et al., 2002]. Coprophagy in ring-tailed lemurs may be an aspect of their ability to adapt to changing environmental conditions and incorporate new feeding opportunities into their diet and may be especially valuable for older individuals.

The implications of coprophagy have the potential to be severe. Humans and their livestock are recent arrivals to Madagascar and they likely have brought new parasites and diseases [Sauther et al., 2006]. By consuming feces from other animals, ring-tailed lemurs may be exposing themselves to human, cow, and dog parasites. Preliminary parasitological analyses of lemur feces have not revealed any differences in types and numbers of parasites between groups that have been observed eating feces and those that do not (M. Hunter-Ishikawa, personal communication). Because lemurs select dry feces, they are potentially limiting their exposure to some human parasites that are not able to survive for extended periods of time in feces. However, lemurs may come into contact with fresh feces while foraging for dried human, dog, and zebu feces. Future research will continue to examine the prevalence of parasitism in ring-tailed lemurs as well as their feeding habits throughout the year to address the impact of coprophagy on the health and long-term survival abilities of ring-tailed lemurs in areas of human encroachment.

During 2005 major changes were made to the camp area [Loudon et al., 2006]. The traditional Mahafaly latrine was discontinued and the area was covered over. The traditional latrine was then moved to an area approximately 1.5 km to the south of the camp. As of 2005, a group of ring-tailed lemurs (Light-Blue group) whose home range encompasses the new latrine are now encountering human fecal matter. However, to date they have not been observed ingesting human, cattle, or dog feces.

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