RESEARCH ARTICLES

The Relationship Between Forage Material and Levels of Coprophagy in Captive Chimpanzees (Pan troglodytes)

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Although coprophagy is practiced in the wild by chimpanzees (Pan troglodytes), it occurs more frequently and under more varied circumstances in captivity. This study was designed to determine if different forage materials and amount of residual undigested grain particles found in the feces might cause an increase in coprophagous behavior in those animals which already exhibited the behavior. A possible effect of availability of seed pits and fibrous leaves for “wadge” making, a typical chimpanzee behavior, on levels of coprophagy was also considered. Observations for coprophagous behavior were conducted on 65 juvenile, adolescent, and adult chimpanzees. Coprophagy levels were significantly lower with popcorn than either chicken scratch or sweet feed. A significant increase in coprophagy was noted for all weeks of forage types when tested against the wadge weeks. Residual grain content analysis showed no significant difference in coprophagous behavior between any of the testing conditions. Decreasing levels of coprophagous behaviors may be assisted by the provision of wadge materials.

Key words: coprophagy, forage, residual grain, Pan troglodytes, grain, wadge

INTRODUCTION

Coprophagy is practiced, to some degree, by both gorillas and chimpanzees in the wild [Goodall, 1986; Harcourt and Stewart, 1978]. Among wild chimpanzees, certain factors seem to be associated with this behavior. Individuals in ill health have been observed to pick through their own feces to consume undigested bits of food and seeds [Goodall, 1986]. Infants imitated the behavior after watching their mothers eat feces. Following meat-eating episodes, chimpanzees have been observed picking...
pieces of undigested flesh out of their feces and consuming them, and have eaten the feces of their prey, according to Goodall [1986].

In captivity, coprophagy occurs much more frequently, and within more varied contexts, than in the wild. The habit seems to be exacerbated by stress and boredom [Akers and Schildkraut, 1985; Hill, 1966]. Boredom may be a result of captivity and the lack of foraging opportunities, which occupy 13% of their day in the wild [Wrangham and Smuts, in Goodall, 1986]. Insufficient dietary roughage for the making of “wadges” may also compel chimpanzees to chew their own feces [Kollar et al. 1968]. Wadge making is a typical chimpanzee activity where some parts of the meal, such as seeds, peelings, and leaves are not swallowed but kept in the mouth between the tongue and palate. They are sucked on, and manipulated with the tongue and lips until all juices are extracted [Goodall, 1986]. They are then discarded. Infants may learn coprophagy from their coprophagic mothers, or begin to practice it following early manipulation and olfactory/gustatory exploration of feces [Hill, 1966]. Once learned, the practice becomes a habit that is extremely difficult to eliminate. A previous study at the Primate Foundation of Arizona (PFA) examined captive chimpanzees’ preference for different forage types. Three forage types were tested and all contributed to increased activity levels. However, the care staff at PFA observed that coprophagy appeared to increase when a particular forage was presented. These observations suggested that the animals were perhaps picking apart and eating feces in order to get at undigested, favored, or interesting grains. In short, perhaps they were practicing a natural behavior, but to a much greater degree than is seen in the wild.

This present study examined the same three forage materials to confirm the care staff observation and to determine if a particular forage type influenced levels of coprophagy. Because of the known beneficial increase in activity levels with forage, materials other than forage and known to be favored wadge material were provided with a grain type and then alone to note if coprophagy levels might decrease by its presence. Amount of “residual,” undigested grain particles found in the feces was also analyzed to see if a particular grain could be identified as one that increased coprophagy.

MATERIALS AND METHODS

Subjects

The subjects of this study were 65 captive chimpanzees at PFA. The sample consisted of 39 females and 26 males, ranging in age from 10 months to 36 years. The subjects were housed in 14 different social groups with the exception of 3 animals that were singly housed but had olfactory, visual, auditory, and tactile contact with adjacent and neighboring chimpanzees.

Procedure

Three types of forage material were provided: chicken scratch (consisting of milo, cracked corn, and wheat), sweet feed (consisting of rolled corn, rolled barley, and a small amount of molasses), and popcorn (unsalted and hot-air popped). These materials had been demonstrated in the previous study to be desirable. A single forage type was provided daily for seven days beginning on a Monday as follows: popcorn during week 1, chicken scratch during week 2, sweet feed during week 3. The forage
material found to be the most cost-effective, sweet feed, was presented with several types of wadge for week 4. Wadge material included fruit pits, palm frond stems, and corn cobs. The pits and corn cobs were food residuals, while the stem of the palm frond is specifically provided as wadge material. Week 5, only wadge with no forage was distributed.

The forage material was distributed every morning between 8:30 A.M. and 11:00 A.M. following the morning feeding of fruit. One of two distribution methods was employed: (1) the bedding material comprised of straw and sawdust was hand-seeded with the designated forage; or (2) forage was distributed from a “blowing device,” constructed by attaching a PVC tube to the reverse outlet of a vacuum cleaner. The tube had a port through which the forage material could be poured. Both methods allowed the material to be evenly distributed in the straw and sawdust bedding throughout the cage. Amount of forage distributed was determined by group size and average age. Adults were housed in social groups of four or less; juveniles and adolescents were housed in larger groups. In social groups consisting of fewer than four chimpanzees, 11 ounces of chicken scratch, 8 ounces of sweet feed, or 2 ounces of popcorn (weight before popping) were distributed for each individual. Juvenile and adolescent groups received slightly less forage grains and wadge. Apart from the forage material distributed, daily diet consisted of 2–4 citrus fruits (oranges or grapefruit), 2–4 apples, 1 banana, and pieces of cantaloupe when available for breakfast. Lunch was 1/4 head of cabbage, 1 carrot, 1/2 onion, 1/2 sweet potato, 1–2 tomatoes, and, when available, portions of broccoli, cauliflower, green beans, corn, and celery. In the evenings, 1 pound of standard primate chow was fed to each individual.

A daily observation form listing the individuals in each social group was used to record coprophagy. Daily one-zero sampling for coprophagous activity was divided into morning (8:00 A.M. to 12:00 P.M.) and afternoon (1:00 P.M. to 5:00 P.M.) time frames. The score for each subject was the proportion of days on which coprophagy was observed. Observations were made Monday through Friday by 16 animal care personnel and research staff. Given the large number of scorers and their very frequent contacts daily with all groups, we assumed that the subjects were observed a minimum of four times during each hour. Coprophagy was defined as active oral contact with fecal matter. This included eating feces, carrying feces in the mouth, and smearing feces with the lips or mouth. Coprophagy was not recorded if feces were merely visible on the lips and no oral manipulation was observed. Before commencement of the study, all scorers reached agreement on the definition of coprophagic behavior as defined for this study. When coprophagy was observed, a check was placed by the animal’s name in the appropriate daily morning or afternoon cell on the observation form.

Because the majority of the animals were housed in groups, precise measurement of each individual’s passage of grain in feces could not be measured. To approximate an index of fecal grain content, fecal samples were collected from each social group of animals every other day, Tuesday through Sunday. Fecal samples were not collected on Mondays, the first day of a new grain cycle, to allow time for passage of grains distributed in the previous cycle. Three fecal samples were collected per social group, per grain type. All samples were placed in small individual plastic bags, labelled by location, and weighed to the nearest centigram. The total wet weight
of the sample minus the weight of the plastic bag was recorded as Fecal Weight. Samples were kept frozen until they could be screened.

For screening, each sample was placed on a 1/4” shaker screen tray and washed with water until only undigested material remained. All excess water was removed by gently shaking the tray. The undigested material was collected, weighed, and identified.

Undigested material was then placed on a plastic surface and all particles of the specific grain type fed that week were manually removed with a pair of thumb forceps. These particles were weighed and recorded as Total Wet Grain Weight. If grain particles from the previous cycle were present, these also were separated out, weighed, and recorded. However, they were not included in the Total Grain Weight. If grain particles were too fine to manually separate from other undigestible material, as was usually the case with popcorn, the Total Grain Weight was recorded as ‘‘trace’’ and the grain content was described in the log. Prior to data analysis, these ‘‘trace’’ notations were converted to a grain weight by the following formula: the smallest grain weights measured over the course of the study were .001 percent of the total fecal weight recorded for those samples. Where ‘‘trace’’ was recorded, the total fecal weight was multiplied by .001 to obtain a residual grain weight. The percent fecal grain content for all samples was obtained by dividing the wet weight of the undigested grains by the total wet weight of the fecal sample.

Analyses

For each individual, in each grain week, the proportion of days during which coprophagy was observed was calculated. This proportion was treated as the coprophagy score. Individuals who exhibited no coprophagous activity in any grain week or who were removed from their social group during the study were dropped from analysis at this point. This reduced the sample size to 50 (22 males, ages 11 months to 23 years, and 28 females, ages 10 months to 36 years). Thus, the results are pertinent only to members of the population who, at some time, engage in coprophagy.

The Friedman two-way analysis of variance by ranks, subjects = 50 and K = 5 conditions, was used to test the null hypothesis that the different grain types had no effect on the level of coprophagy. Given a significant Friedman’s ANOVA Statistic (Fr), multiple comparisons between grain types were run to determine where the difference lay [Siegel and Castellan, 1988]. Similar analysis was run on fecal grain content per condition per social group, using social group (n = 14) as the unit of analysis. Multiple comparisons between grain types were also run, if a significant Fr was found. The association between fecal grain content and amount of coprophagous activity was tested by Pearson Correlation Coefficient.

RESULTS

The Friedman two-way analysis of variance by ranks showed that there was systematic variation in the rankings across the different weeks between individuals in the amount of coprophagic behavior (Fr = 30.564, P < 0.001). Multiple comparisons found four conditions to differ significantly (P < 0.05): chicken scratch week (x̄ = .18) and sweet feed with wadge work (x̄ = .07); chicken scratch week (x̄ = .18) and wadge only week (x̄ = .04); sweet feed week (x̄ = .16) and sweet feed with
TABLE 1. Means and standard deviations of coprophagy behavior and fecal grain content

<table>
<thead>
<tr>
<th>Condition</th>
<th>Coprophagy mean (sd) (n = 50)</th>
<th>Fecal grain mean (sd) (n = 14)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Popcorn</td>
<td>0.111 (.16)</td>
<td>0.071 (.04)</td>
</tr>
<tr>
<td>Chicken scratch</td>
<td>0.180 (.18)</td>
<td>1.209 (1.06)</td>
</tr>
<tr>
<td>Sweet feed</td>
<td>0.163 (.19)</td>
<td>0.0342 (0.25)</td>
</tr>
<tr>
<td>Sweet feed w/wadge</td>
<td>0.066 (.14)</td>
<td>0.087 (0.06)</td>
</tr>
<tr>
<td>Wadge only</td>
<td>0.043 (.09)</td>
<td>0.000 (0.00)</td>
</tr>
</tbody>
</table>

The Friedman two-way analysis of variance by ranks tested the effect of the amount of residual grain found in the feces among the 14 different groups and revealed that fecal grain content differed significantly ($Fr = 41.157, P < 0.05$). Multiple comparisons showed that fecal grain content was significantly higher during chicken scratch week ($\bar{x} = 1.2$) when compared to all other conditions. There was also a significant difference between popcorn week ($\bar{x} = .07$) and wadge only week ($\bar{x} = .04$); sweet feed week ($\bar{x} = .34$) and wadge only week ($\bar{x} = .00$); and sweet feed with wadge week ($\bar{x} = .09$) and wadge only week ($\bar{x} = .00$).

The association between fecal grain content and amount of coprophagous activity was tested by Pearson's Correlation Coefficient. A coprophagy score was calculated for each individual subject by grain week. A "condition" fecal grain content score was calculated as the means of the 3 samples from each social group. These coprophagy scores were correlated with fecal grain content. The correlation between coprophagy and fecal grain content was extremely low and insignificant.

DISCUSSION

The results support the hypothesis that grain type and coprophagic behavior may be associated. Coprophagy scores were higher when chicken scratch or sweet feed were available than when popcorn was available. Residual grain content was higher when chicken scratch and sweet feed were present than when popcorn or wadge only were available. However, there was no significant correlation between coprophagous activity and residual grain content. The method of collecting fecal grain content per social group may have been too insensitive to conclude there is no association between coprophagous activity and residual grain content. However, helpful management guidelines can be gained from the analysis.

Important benefits have been shown to result from providing foraging grains and other forage materials for captive primates: among them, decreased rates of aggression [Anderson and Chamove, 1984] and increased activity rates [Maki et al., 1989; Maki and Bloomsmith, 1989; Tripp, 1985]. The results of this study show that, while it may not be possible to identify a single "bad" grain, provision of different forage types may increase coprophagy.

Levels of coprophagy may be lowered by offering wadging materials simultaneously with the forage. In addition to corn cobs, fruit pits, and palm frond stems...
(very fibrous material), PFA has found such items as cardboard and fruit peels to be favored for wadge making by the chimpanzees. Kollar et al. [1968] reported that 70\% of the “free-ranging” chimpanzees living in a 30-acre enclosure in the New Mexico desert were coprophagic and they attributed this to lack of dietary roughage. According to their report, deprived animals may turn to their own body products to meet the need for a chewing wadge. They further noted that very little of the fecal matter was actually consumed. Provision of wadge materials may assist in reducing levels of coprophagy, while allowing activity inducing forage materials to be provisioned.

CONCLUSIONS

1. Higher levels of coprophagy were noted when forage grains were present than when they were not.
2. Wadge materials in a captive chimpanzee’s cage may reduce coprophagous behavior.
3. Foraging for small food types simulates a species-typical behavior in captive chimpanzees. Although foraging for certain grain types may increase coprophagy, simultaneously provisioning of a wadge material may decrease it.

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