LM Hopper, HD Freeman & SR Ross (2016) 
Reconsidering coprophagy as an indicator of negative welfare for captive chimpanzees. 
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Abstract

For captive chimpanzees, ‘abnormal’ behaviors include behaviors observed only in captivity (i.e. species-atypical behaviors) and those that are performed at higher rates in captivity compared to in the wild. Both types are used as metrics for evaluating captive primates’ welfare. However, categorizing all abnormal behaviors together ignores variation in their etiologies, which limits our ability to understand them and provide useful interventions. Coprophagy (deliberately eating feces) is an intriguing abnormal behavior because, unlike many abnormal behaviors, it is performed at higher rates among captive chimpanzees that were mother reared, compared to those that were human reared, and it has been pro-posed that it represents a socially learnt ‘cultural’ behavior. Furthermore, coprophagy is observed among both wild and captive animals, although at higher rates in captivity. Typically, coprophagy is classed with other abnormal behaviors by those evaluating captive chimpanzee welfare, but such categorization has arisen from a top-down approach based on a priori assumptions. To apply a bottom-up approach, which would allow us to identify relations between behaviors in chimpanzees’ repertoire, in this study we ran a principal components analysis on the behaviors performed by 60 captive chimpanzees, to determine whether coprophagy should be classified with other abnormal behaviors. The principal components analysis revealed seven factors that we termed social, aggressive, playful, active, feed, abnormal and self-directed. Furthermore, the analysis revealed that coprophagy loaded onto the ‘social’ factor, which included positive social behaviors, and not onto the ‘abnormal’ factor, which included other abnormal behaviors. Supporting previous research, we also found that those chimpanzees that were mother-reared showed higher rates of coprophagy than those that were human reared; there was a significant positive correlation between time spent with conspecifics during the first four years of life and the rate of coprophagy performed by the subjects as adults (r = 0.575, N = 60, P < 0.001). We discuss these results giving consideration to the practical applications for monitoring and evaluating captive chimpanzee welfare and also from a theoretical perspective about the social learning mechanisms that may underpin the transmission of coprophagy among captive chimpanzees.
What Are Abnormal Behaviors?

- Species atypical behaviors
- Behaviors performed at different frequencies in captivity vs. the wild
- May indicate compromised welfare

Poke Eye
Bite self
Coprophagy
Rocking
Regurgitation & Reingestion

Considering Coprophagy

- Oral manipulation and ingestion of feces
- Observed in wild and captive chimpanzees (reportedly higher rates in captivity)
- Typically classed as an abnormal behavior

Coprophagy May Be Different

• Seen in mother-reared captive chimpanzees more than human-reared chimpanzees

• Proposed to be a potentially socially-learned (‘cultural’) behavior

The Chimpanzees We Studied

- 60 chimpanzees living in 9 US accredited zoos and sanctuaries
  - 25 Males, 35 Females, 6-54 years old
  - Captive born and socially housed
- Behavioral data collected using focal follows (1385hrs total observation time)

The Chimpanzees’ Behavior

- 37% of chimpanzees performed coprophagy but in very low rates (0.04%-1.8% of time)

- There was a negative correlation between exposure to humans during early rearing and proportion of time spent performing coprophagy as adults

- Principal Components Analysis revealed coprophagy loaded onto a factor with social, not abnormal, behaviors

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Social</th>
<th>Aggressive</th>
<th>Playful</th>
<th>Active</th>
<th>Feed</th>
<th>Abnormal</th>
<th>Self-directed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prosocial</td>
<td>.782</td>
<td>-0.092</td>
<td>.101</td>
<td>.112</td>
<td>-0.236</td>
<td>.111</td>
<td>-0.129</td>
</tr>
<tr>
<td>Sexual behavior</td>
<td>.769</td>
<td>-0.067</td>
<td>0.003</td>
<td>-0.173</td>
<td>0.044</td>
<td>-0.038</td>
<td>-0.038</td>
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<tr>
<td>Coprophagy</td>
<td>.699</td>
<td>-0.117</td>
<td>-0.133</td>
<td>0.012</td>
<td>0.305</td>
<td>-0.075</td>
<td>-0.204</td>
</tr>
<tr>
<td>Groom (receive)</td>
<td>.668</td>
<td>0.217</td>
<td>-0.227</td>
<td>0.291</td>
<td>0.197</td>
<td>-0.254</td>
<td>0.083</td>
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<tr>
<td>Groom (give)</td>
<td>.467</td>
<td>0.223</td>
<td>-0.325</td>
<td>0.399</td>
<td>0.222</td>
<td>-0.282</td>
<td>-0.008</td>
</tr>
<tr>
<td>Contact Aggression (receive)</td>
<td>-0.018</td>
<td>0.926</td>
<td>0.059</td>
<td>0.042</td>
<td>-0.026</td>
<td>-0.026</td>
<td>0.065</td>
</tr>
<tr>
<td>Noncontact aggression (give)</td>
<td>-0.057</td>
<td>0.888</td>
<td>0.027</td>
<td>0.051</td>
<td>-0.182</td>
<td>0.141</td>
<td>0.112</td>
</tr>
<tr>
<td>Contact aggression (give)</td>
<td>-0.047</td>
<td>0.761</td>
<td>0.206</td>
<td>0.018</td>
<td>0.299</td>
<td>-0.186</td>
<td>-0.096</td>
</tr>
<tr>
<td>Play (social)</td>
<td>0.015</td>
<td>0.075</td>
<td>0.758</td>
<td>0.295</td>
<td>0.321</td>
<td>-0.032</td>
<td>-0.104</td>
</tr>
<tr>
<td>Play (self)</td>
<td>-0.011</td>
<td>-0.026</td>
<td>0.730</td>
<td>0.172</td>
<td>-0.025</td>
<td>0.103</td>
<td>-0.082</td>
</tr>
<tr>
<td>Noncontact aggression (receive)</td>
<td>-0.136</td>
<td>0.177</td>
<td>0.649</td>
<td>-0.266</td>
<td>0.140</td>
<td>-0.220</td>
<td>-0.018</td>
</tr>
<tr>
<td>Masturbation</td>
<td>-0.071</td>
<td>0.252</td>
<td>0.598</td>
<td>-0.287</td>
<td>-0.325</td>
<td>-0.110</td>
<td>0.186</td>
</tr>
<tr>
<td>Inactive</td>
<td>-0.096</td>
<td>-0.149</td>
<td>-0.130</td>
<td>-0.864</td>
<td>-0.183</td>
<td>-0.140</td>
<td>-0.148</td>
</tr>
<tr>
<td>Locomotion</td>
<td>0.002</td>
<td>-0.076</td>
<td>0.016</td>
<td>0.725</td>
<td>-0.166</td>
<td>-0.185</td>
<td>0.157</td>
</tr>
<tr>
<td>Attention</td>
<td>-0.373</td>
<td>0.158</td>
<td>-0.040</td>
<td>0.472</td>
<td>-0.404</td>
<td>0.086</td>
<td>-0.385</td>
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<tr>
<td>Feed/forage</td>
<td>-0.016</td>
<td>0.120</td>
<td>0.097</td>
<td>-0.048</td>
<td>0.826</td>
<td>0.035</td>
<td>-0.041</td>
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<td>Submissive</td>
<td>-0.211</td>
<td>0.120</td>
<td>-0.019</td>
<td>-0.048</td>
<td>-0.449</td>
<td>0.126</td>
<td>-0.196</td>
</tr>
<tr>
<td>Abnormal body manipulation</td>
<td>0.018</td>
<td>-0.051</td>
<td>0.061</td>
<td>-0.140</td>
<td>0.292</td>
<td>0.759</td>
<td>0.045</td>
</tr>
<tr>
<td>Abnormal body movement</td>
<td>-0.201</td>
<td>-0.171</td>
<td>-0.094</td>
<td>-0.038</td>
<td>-0.153</td>
<td>0.604</td>
<td>0.035</td>
</tr>
<tr>
<td>Display</td>
<td>0.008</td>
<td>0.156</td>
<td>-0.047</td>
<td>0.091</td>
<td>-0.138</td>
<td>0.592</td>
<td>0.068</td>
</tr>
<tr>
<td>Groom self</td>
<td>-0.145</td>
<td>0.188</td>
<td>0.102</td>
<td>0.201</td>
<td>-0.033</td>
<td>0.049</td>
<td>0.816</td>
</tr>
<tr>
<td>Hair pluck (self or other)</td>
<td>-0.109</td>
<td>-0.043</td>
<td>-0.193</td>
<td>0.054</td>
<td>0.094</td>
<td>0.043</td>
<td>0.769</td>
</tr>
</tbody>
</table>

Cultural Coprophagy?

- Chimpanzees copy arbitrary behaviors from groupmates – what about coprophagy?
- Social proximity to group mates and exposure to conspecifics during early rearing promote social learning; our data revealed that coprophagy is linked to positive social behaviors and that coprophagy was performed more by mother-raised than human-raised chimpanzees.
- In line with previous research, we propose that chimpanzees may socially learn coprophagy, and that it may present a behavior that helps maintain social bonds.
- Next steps: record and evaluate the transmission of coprophagy within and between captive groups of chimpanzees to test for social transmission in real time.

References and Further Reading


• **Freeman HD & Ross SR (2014).** The impact of atypical early histories on pet or performer chimpanzees. *PeerJ* 2, e579.


Acknowledgments

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• If you have questions about this research, please email lhopper@lpzoo.org