



Reconsidering coprophagy as an indicator of negative welfare for captive chimpanzees



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ARTICLE INFO

Article history:

Received 27 August 2015

Received in revised form

31 December 2015

Accepted 4 January 2016

Available online 19 January 2016

Keywords:

Coprophagy

Chimpanzee

Welfare

Abnormal behaviour

Social learning

Captivity

ABSTRACT

For captive chimpanzees, 'abnormal' behaviours include behaviours observed only in captivity (i.e. species-atypical behaviours) 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 behaviours together ignores variation in their etiologies, which limits our ability to understand them and provide useful interventions. Coprophagy (deliberately eating faeces) is an intriguing abnormal behaviour because, unlike many abnormal behaviours, it is performed at higher rates among captive chimpanzees that were mother reared, compared to those that were human reared, and it has been proposed that it represents a socially learnt 'cultural' behaviour. Furthermore, coprophagy is observed among both wild and captive animals, although at higher rates in captivity. Typically, coprophagy is classed with other abnormal behaviours 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 behaviours in chimpanzees' repertoire, in this study we ran a principal components analysis on the behaviours performed by 60 captive chimpanzees, to determine whether coprophagy should be classified with other abnormal behaviours. 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 behaviours, and not onto the 'abnormal' factor, which included other abnormal behaviours. 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.

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1. Introduction

The manner in which the behavioural repertoire of captive primates differs from that shown by their wild counterparts has been a cornerstone of defining 'normal' and 'abnormal' behaviour for these animals. Deviations from the typical repertoire of a wild animal observed in captive primates is most often interpreted as being problematic and possibly an indicator of a compromised welfare state (e.g. Birkett and Newton-Fisher, 2011). Captive primate behaviour may differ from wild primate behaviour in two key ways:

(i) the form or type of a given behaviour, or (ii) the frequency or rate of a given behaviour. Traditionally, both forms of deviation, that of form and that of frequency, have been lumped together as abnormal behaviour, when in fact there may be reason to consider them distinctly. For example, captive apes have been reported to produce vocalizations that differ in acoustic structure or usage from the vocalizations of wild apes (e.g. Hopkins et al., 2007; Wich et al., 2009), but although these vocalizations are not species typical, they are not typically recorded as 'abnormal' behaviours by those evaluating captive ape welfare (e.g. Marriner and Drickamer, 1994; Birkett and Newton-Fisher, 2011; Freeman and Ross, 2014; Llorente et al., 2015). In contrast, other behaviours seen only in captive populations, such as repetitive rocking, are considered both as abnormal and as indicators of negative welfare (e.g. Fritz et al.,

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1992b). Therefore, simply because a behaviour may be restricted to the repertoire of captive primates does not automatically mean it has negative welfare connotations.

In addition to behaviours only seen in captivity (i.e. species-atypical behaviours), it has been argued that species-typical behaviours should also be classified as abnormal if recorded at very different rates in captivity (Birkett and Newton-Fisher, 2011). Specifically, Akers and Schildkraut (1985) noted that such behaviours are “in a statistical sense, normal for captive populations . . . [but] abnormal when compared to the animals’ natural behaviours in the wild, where the peculiar behaviours are rare or absent” (p. 99). Such behaviours include regurgitation and reingestion (Akers and Schildkraut, 1985; Baker and Easley, 1996) and coprophagy (Fritz et al., 1992a; Fish et al., 2007; Bertolani and Pruetz, 2011), which are performed by wild primates, but are reportedly performed at higher rates by captive animals. It is still poorly understood why certain behaviours are performed at elevated rates in a captive setting, and whether an increase in occurrence is universally negative (Ross and Bloomsmith, 2011), as the relationship between observed stereotypic behaviour and welfare is convoluted (Mason and Latham, 2004).

The classification of coprophagy, the deliberate ingestion of feces, as a behaviour indicative of compromised welfare has arisen from a top-down process relying on a priori assumptions rather than from a bottom-up approach which seeks to create categorizations based on the intrinsic value of the items. Because coprophagy fits the umbrella category as ‘differing from the norm,’ it is categorized with other atypical behaviours used as indicators of poor welfare (e.g. Birkett and Newton-Fisher, 2011; Freeman and Ross, 2014; Lorente et al., 2015). An alternative approach is to categorize behaviours based on their relationships to each other, their etiologies, or their environmental correlates, thereby more directly evaluating their usefulness as metrics of wellbeing (see, for example, Bashaw et al., 2001). This is especially vital for behaviours classed as abnormal that are observed both in captive and wild populations, because it is important to understand why these behaviours are observed at higher rates in captivity and whether this increase in rate is a meaningful indicator of welfare.

Distinguishing coprophagy from negative abnormal behaviours might be important for two key reasons. First, different abnormal behaviours may have different etiologies. Encoding multiple behaviours within the umbrella term ‘abnormal behaviours’ (c.f. Wood, 1998), misses variance that could be crucial to identifying underlying causes of certain behaviours and determining the impact of interventions (e.g. the provision of enrichment, Shyne, 2006), which may influence the expression each behaviour differently. Given that coprophagy is seen more commonly among mother-reared than human-reared chimpanzees suggests a separate underlying cause compared to other abnormal or stereotypical behaviours, such as body rocking, which are often symptomatic of atypical rearing histories (Spijkerman et al., 1994; Martin, 2002). Second, if coprophagy is not an abnormal behaviour that is indicative of negative welfare, then, for theoretical and practical reasons, classifying coprophagy as a negative abnormal behaviour has limited value. Theoretically, it undermines our interpretation of chimpanzee behaviour and, practically, observations of coprophagy may not be as useful a tool for measuring welfare compared to recording rates of other abnormal behaviours (e.g. self-injurious behaviour).

To address this, we used a principal component analysis to gain a deeper understanding of the relationship between chimpanzee behaviours categorized as ‘abnormal’ (with a particular emphasis on coprophagy) and species-typical behaviours observed among captive chimpanzees. Principal component analyses are useful because they can reveal commonalities among separate items; in this case, behaviours. Previously, such analyses have

been used to define behaviour from both observer-generated terms (i.e. ‘free choice profiling’, Wemelsfelder et al., 2001; Rutherford et al., 2012) and from behavioural items (de Passillé et al., 1995). Considering captive chimpanzees specifically, studies employing principal component analyses have revealed components of personality derived from questionnaire scores (Morton et al., 2013) and from behavioural observations (Massen et al., 2013), and have been used to investigate the relationship between chimpanzee personality ratings and their behavioural repertoire (Freeman et al., 2013).

In this study, we observed the behaviour of 60 captive chimpanzees housed in nine different facilities and used a principal component analysis to determine what factors emerged from the behaviours we recorded. Our aim was to determine whether coprophagy loaded onto a factor with other (negative) abnormal behaviours following ethograms typically used to describe captive primate behaviour and so, in addition to coprophagy, we recorded the frequency of the following abnormal behaviours as part of our ethogram: regurgitation and reingestion, urophagy, hair plucking, idiosyncratic body manipulations and idiosyncratic body movements. Given the increased rates of coprophagy reported for mother-raised captive chimpanzees, and our hypothesis that coprophagy, although abnormal, should not be considered as an indicator of negative welfare, we predicted that coprophagy would not load onto a factor with other abnormal behaviours. As it has been suggested that coprophagy might be a socially-learned and potentially a ‘cultural’ behaviour (Hook et al., 2002; Freeman and Ross, 2014), we predicted that coprophagy might load onto a factor that was comprised of social behaviours (e.g. grooming) as social proximity and positive social relationships are known to promote social learning among chimpanzees (Bonnie and de Waal, 2006; Hobaiter et al., 2014). We also predicted that higher rates of coprophagy would be shown by chimpanzees who had been reared with other conspecifics compared to human-raised chimpanzees.

2. Methods

This study was approved by and complied with protocols approved by the Chimpanzee Species Survival Plan management group for the Association of Zoos and Aquariums, the Lincoln Park Zoo Research Committee, and the animal care committees at each of the institutions that participated in this study.

2.1. Subjects and housing

The subjects for this study were 60 chimpanzees (25 males, 35 females, mean age = 21 years, range: 6–54 years) which were housed at nine different facilities within the USA. Thirty-seven of the chimpanzees were housed in zoos accredited by the Association of Zoos and Aquariums ($N=6$) and 23 of the chimpanzees were housed in sanctuaries that were members of the North American Primate Sanctuary Alliance ($N=3$). All of the chimpanzees in the study were captive-born and all were socially housed. The chimpanzees at each of the facilities had both indoor and outdoor access. The indoor areas were all rooms comprised of concrete floors with elevated benches and all facilities provided enrichment and nesting materials in both the indoor and outdoor enclosures, although the specific type and quantity varied by facility. The size of the enclosures that the chimpanzees lived in was also different across the nine facilities, but the average enclosure size was 3855 m². Although the diet of the 60 chimpanzees varied by facility, the chimpanzees were all provided daily with primate chow and fruit and/or vegetable food enrichment at each of the facilities. For the purposes of this study, it is important to note that none of the chim-

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