The influence of sex, rearing history, and personality on abnormal behaviour in zoo-housed bonobos (Pan paniscus)

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Abstract

Abnormal behaviours are often used as a welfare indicator in zoo-housed great apes. While previous studies report on the occurrence of abnormal behaviours in zoo-housed chimpanzees (*Pan troglodytes*), there is currently a lack of knowledge about such behaviours in the closely related bonobo (*Pan paniscus*). Here we report on the prevalence, diversity and frequency of abnormal behaviours, based on 1531 hours of observations in 51 adult bonobos, living in six zoos. We also investigate the potential influence of age, sex, rearing history and four previously established personality traits (Activity, Boldness, Openness and Sociability) on the diversity and frequency of abnormal behaviours. Our results document the presence of a total of 13 abnormal behaviours in the population, with the five most frequent ones being *Coprophagy*, *Poke anus*, *Social hair pluck*, *Regurgitation* and *Head shake*. We find that wild-born bonobos show a higher diversity of abnormal behaviours compared to mother-reared individuals, likely due to their abnormal early-life experiences. Mother-reared individuals and males show lower frequencies of *Poke anus*. The frequency of abnormal behaviours is also linked to personality. Bonobos scoring lower on Activity, associated with more self-scratching and lower activity, engage more in *Coprophagy* and *Head shaking*. More sociable individuals, on the other hand, had higher frequencies of *Social hair pluck*, which follows a previous finding that this behaviour is embedded in grooming. Finally, more sociable individuals also had lower frequencies of *Coprophagy*, an indicator that higher sociability might cause higher resilience to stressors. Our study provides a first overview of the abnormal behaviours in zoo-housed bonobos. We discuss that not all abnormal behaviours may be suitable indicators of poor welfare. These results form an important base in our understanding of the repertoire of abnormal behaviours in zoo-housed bonobos, which is a crucial step for optimising their welfare.

Keywords (indexing terms)

Abnormal behaviour; Animal welfare; Great ape; Rearing; Personality; Zoo.

1. Introduction

Abnormal behaviours in captive animals are defined as those that deviate qualitatively (i.e. by kind) or quantitatively (i.e. by degree) from behaviours observed in wild-living individuals (Birkett and Newton-Fisher, 2011; Bloomsmith et al., 2019; Wallace et al., 2019). Factors that may trigger the development of abnormal behaviours include the inability to perform species-specific behaviours (Browning, 2019; Clubb and Mason, 2007), lack of environmental control (Hosey, 2005) and atypical social experiences, like the absence of maternal care during early-life periods or limited contact to conspecifics (Bellanca and Crockett, 2002; Freeman and Ross, 2014). In contrast, attempts to improve the welfare of animals can reduce abnormal behaviours, for example through positive reinforcement training (Pomerantz and Terkel, 2009), more complex and naturalistic enclosure designs (Ross et al., 2010) and enrichment programs (Mason et al., 2007; Swaisgood and Shepherdson, 2005).

Behaviour, in general, is currently the most used parameter to assess zoo animal welfare (Binding et al., 2020) and because abnormal behaviours often arise as a result of past or present suboptimal (social) conditions, they are often used as an indicator for negative welfare (Mason, 1991). Despite their importance in identifying potential welfare issues (Dawkins, 2015; Rose et al., 2017), the study of abnormal behaviours remains challenging (Mason and Latham, 2004). One major difficulty is identifying their underlying aetiologies and assessing their actual effect on the psychological wellbeing of the animal. Behaviours that are relatively well-understood in terms of their impact on animal welfare include self-injurious behaviours which are linked to early life stressors such as maternal separation (Novak et al., 2013; Polanco, 2016) and abnormal repetitive behaviours which are associated to a failure to cope with stressful events or environments (Bacon, 2018; Rose et al., 2017). Yet, for many other behaviours considered abnormal, the evidence is lacking to associate them with the animal's welfare. On top of that, some abnormal behaviours are socially learnt (Hook et al., 2002; Hopper et al., 2016) and as such their presence no longer represents a response to stressors.

Interestingly, the occurrence of abnormal behaviour varies between individuals within a specific environment. Studying what factors are associated with patterns of abnormal behaviours can help to better understand their aetiologies and can help to inform welfare practices. Factors including sex, age and the species itself are linked to abnormal behaviours (Bloomsmith et al., 2019; Kummrow and Brüne, 2018; Lutz, 2018). For example, studies on nonhuman primates report that males perform more abnormal behaviours in general (Mallapur and Choudhury, 2003; Trollope, 1977). However, a recent study on a large sample of two macaques species (*Macaca fascicularis* and *Macaca mulatta*) and baboons (*Papio hamadryas*) report that male macaques exhibited more abnormal appetitive behaviours while in baboons, the females exhibited more of these behaviours (Lutz, 2018). Age also influences abnormal behaviour, especially on active abnormal behaviours (e.g. motor stereotypies) since these can be linked to the animal's physical abilities. More physically active stereotypical behaviours sometimes decrease with age, as shown in macaques (Gottlieb et al., 2013, 2015; Lutz, 2018) but not in baboons (Lutz, 2018), while other behaviours such as self-directed behaviours and self-injurious behaviours increase with age (Lutz et al., 2003).

Additionally, the individual's personality can play a role. Defined as contextually and temporally consistent differences in the behaviour across individual members of the same species, personalities are known to have a physiological basis (Koolhaas et al., 1999) and as such are associated with the sensitivity to environmental challenges (Carere et al., 2010; Nettle, 2006). Personality is described in a wide range of taxa, including amphibians (Kelleher et al., 2018), insects (Amat et al., 2018), fish (Toms et al., 2010), birds (Groothuis and Carere, 2005), felids (Gartner and Weiss, 2013) and non-human primates (Freeman and Gosling, 2010). Yet, few studies to date have investigated the link between abnormal behaviour and personality. Motor stereotypic behaviours are linked to personality traits characterised by heightened activity in rhesus macaques (*Macaca mulatta*) (Gottlieb et al., 2013) and are more frequent in bold individuals (Gottlieb et al., 2015). Anxious and/or inhibited rhesus macaques also experience more hair loss, likely through a higher expression of self hair plucking (Coleman et al., 2017). In orange winged Amazon parrots (*Amazona* *amazonica*), neuroticism-like traits are linked to feather damaging behaviour, while more extraverted birds were more resilient to environmental stress as they developed less diverse and less frequent stereotypical behaviours (Cussen and Mench, 2014).

Abnormal behaviours are species-specific as are the risk factors that are associated with their occurrence. According to a survey including 68 primate species across 108 zoos, apes more frequently show abnormal behaviours (Bollen and Novak, 2000). Most studies on great ape abnormal behaviour have focused on chimpanzees (*Pan troglodytes*) (Kummrow and Brüne, 2018), of which a majority of the individuals show at least one abnormal behaviour (Birkett and Newton-Fisher, 2011; Bloomsmith et al., 2019; Jacobson et al., 2016). A large-scale cross-zoological study on abnormal behaviour in the closely related bonobo (*Pan paniscus*) is currently lacking, despite some studies reporting on the presence of abnormal behaviours (e.g. Brand et al., 2016; Brand and Marchant, 2018; Miller and Tobey, 2012).

As such, the first aim of this study is to investigate the prevalence, diversity and frequency of abnormal behaviours in a large multi-group sample of bonobos across European zoological institutions. The second aim of our study is to examine potential links between intrinsic factors, such as age, sex, rearing and personality with the occurrence of abnormal behaviour. Specifically, while most previous studies linked such factors to the prevalence of abnormal behaviours, we were interested in assessing their link to the frequency as this might provide additional information regarding the impact on the animal's welfare (Bloomsmith et al., 2019; Brilot et al., 2010; Pomerantz et al., 2012). Together, the goal of this study was to create a first overview of abnormal behaviour in bonobos across zoos and to make an initial attempt to understand which factors may contribute to their occurrence, so that this can be used in future management decisions.

2. Material studied, area descriptions, methods, techniques and ethical approval

2.1. Subjects and housing

Behavioural data were collected between October 2011 and April 2014 on 51 adolescent and adult captive bonobos (32 females and 19 males, Table 1), housed in six European zoological parks. The care and housing of all bonobos was adherent to the guidelines of the EAZA Ex-situ Program (EEP). All individuals were socially housed in a multi-male/multi-female structure (median group size = 10; range 6 - 16) with juveniles and/or infants. Information about the bonobos, including their sex, age and rearing history were collected from the International Studbook (Stevens and Pereboom, 2020). The age of the adult individuals ranged from 7-63 years old, with a median of 21 years. The behaviour of infants and juveniles (age <7) was not scored in this project.

Table 1: Bonobos in study sample within each sex and rearing category.

	Number of individuals	Percentage of the population
Sex		
Female	32	62.7%
Male	19	37.3%
Rearing		
Mother	34	66.7%
Hand	7	13.7%
Wild	10	19.6%

2.2. Data collection

We used the Observer (Noldus version XT 10) to score general behavioural patterns of the 51 individuals using 10 min focals, totalling on average for 29.5 h of observation time per animal (ranging between 12.9-58.2 h per individual) (Altmann, 1974) for a total of 1531.8 h. We selected 28 abnormal behaviours (Table 2), based on an earlier and similar study on chimpanzees in zoos (Birkett and Newton-Fisher, 2011). Our aim was to give an overview of all possible abnormal behaviour in bonobos and as such opted for an inclusive approach and record all behaviours that traditionally have been considered as abnormal. Data were collected by eight observers over 1-3 observation periods per location. Inter-observer reliabilities were calculated based on two 10-minute focal videos that were scored by all observers and reached a Spearman rank correlation mean of $r = 0.87$ across all observers, and so the observations across observers were highly reliable (Martin and Bateson, 1993).

Table 2: Abnormal behaviours used in this study. Behaviours in bold were observed during the observation period and are ordered based on prevalence.

Abnormal behaviour	Definition	Number of zoos in which the behaviour was observed
Coprophagy	**Ingest own or other's faeces**	**6/6**
Poke anus	**Insert finger into own anus**	**6/6**
Social hair pluck	**Pulls out hair of other**	**4/6**
Regurgitate	**Vomit voluntarily, then usually re-ingest vomitus**	**5/6**
Head shake	**Repeatedly shaking head**	**6/6**
Self hair pluck	**Pulls out own hair**	**6/6**
Twirl	**Rotate torso on axis for 360 degrees while upright and bipedal**	**6/6**
Drink urine	**Drink own urine**	**2/6**
Posturing	**Deviating posturing without apparent reason**	**3/6**
Flip lip	**Repeatedly flip lower lip outside**	**3/6**
Head toss	**Circular movement of head**	**3/6**
Rock	**Sway repetitively and rhythmically. Usually side-to-side movement, not exclusively. Usually whole body, sometimes just the head.**	**2/6**
Clap hands	**Slap palm of hand or sole of foot, making noise**	**1/6**
Auto-aggression	Act aggressively towards own	0/6
Cling	Clutch own body or object	0/6
Ear cover	Cover one or two ears with hands	0/6
Eye poke	Poke one or more fingers into own eye	0/6
Genital pat	Touch own genitals	0/6
Head bang	Hit own head against solid surface	0/6
Pace	Locomote, usually quadrupedally, on substrate, covering and then re-covering route in stylised fashion, with no clear objective	0/6
Raspberry vocalisation	Push lips together and produce sound similar to flatulence	0/6
Repetitive body movement	Repeatedly moving body part without apparent function	0/6
Self-mutilation	Self-mutilates repeatedly	0/6
Self-slap	Hit self repeatedly	0/6
Spit	Expel saliva through pursed lips	0/6
Stick out tongue	Repeatedly stick out tongue	0/6
Suck self	Suck own body parts, e.g. finger or toes	0/6
Throw	Throw food object to other	0/6

2.3. Statistics

2.3.1. Descriptive measures of abnormal behaviour

To describe the abnormal behaviour in zoo-living bonobos we analysed four aspects: 1) the prevalence (i.e. the proportion of individuals that perform a certain abnormal behaviour in contrast to the total number of individuals); 2) the diversity (i.e. the total number of different abnormal behaviours one individual shows); 3) the frequency of all abnormal behaviours combined (i.e. the total number of occurrences of all abnormal behaviours per hour per individual) and 4) the frequency of single abnormal behaviours (i.e. the number of occurrences of single abnormal behaviours per hour per individual). Because some behaviours were coded as events, we did not analyse the duration or proportion for all abnormal behaviours and therefore focus on their frequency.

2.3.2. Personality measures

For 41 bonobos that we collected data on abnormal behaviour on, we used personality profiles that were available from a previous study and constructed based on data that was collected at the same time as the abnormal behaviour data (Staes et al., 2016). The personality profiles were constructed using concurrent naturalistic observations and observations from experimental settings. These included 17 behavioural variables (10 from the naturalistic context and 7 from the experimental contexts) but did not include any of the abnormal behaviours studied here. Data were collected in two consecutive years, allowing to test for temporal consistency using intraclass correlations to determine temporal stability. Only stable variables were used to determine personality structure. Dimension reduction analysis on these variables revealed four factors: Activity, Boldness, Openness and Sociability. Details of the item's loading onto each dimension are shown in Table S1. Items that showed cross-loadings >|0.4| on multiple components, were considered part of the dimension on which they had the highest loading (Table 3).

Table 3: Behavioural contents of the personality traits.

Factor	Adjectives loading on to factors
Sociability	+ Grooming frequencies + Grooming density + Neighbours + Grooming diversity − Latency to approach puzzles/durian − Autogroom

Openness	+ Approaches to puzzles/others + Play + Proximity to puzzles + Taste pasta
Boldness	+ Approaches to leopard + Displays to leopard + Proximity to leopard + Aggression received
Activity	+ Activity − Self-scratching

2.3.3. Factors influencing abnormal behaviour

We used Generalised Linear Mixed Models (GLMMs) with backwards selection to identify factors that explain variation in 1) the individual diversity of abnormal behaviour, 2) the frequency of abnormal behaviours combined and 3) the frequency of the most prevalent single abnormal behaviours. To ensure statistical reliability, we only ran GLMMs for single abnormal behaviours that were performed by at least 20 individuals. This criterion was reached for the behaviours *Coprophagy, Poke anus, Social hair pluck, Regurgitation* and *Head shake*. Explanatory factors included in our models were age, sex (female, male), rearing history (mother-reared, hand-reared and wild-born) and four personality traits (Activity, Boldness, Openness and Sociability). Our dataset for the GLMM analyses was restricted to the individuals for whom we had information for all the independent variables, which we had for 41 individuals. We removed any outliers from our dataset (more than 4 SD above the mean). The models assessing the frequency of abnormal behaviours used a negative binomial distribution and a log link function and included the number of observation hours as offset to correct for sampling effort. For the model assessing the diversity of abnormal behaviours, we used a beta distribution with a logit link function. For descriptive measures and figures of the diversity of abnormal behaviour, we report the actual count data. All models included the identity of the subject as random factor to correct for repeated measures. Multicollinearity between independent variables was tested with a variance inflation factor (VIF) threshold of >5 (O'Brien, 2007), but the variables did not show multicollinearity. All analyses were performed using R 2.15.2 (R Core Team, 2016), with the GLMM calculated using the *glmmTMB* package (Brooks et al., 2017). Diagnostic plots (residuals vs. fitted and QQ plots) were used to examine assumptions of normality and homogeneity of variances and we additionally tested uniformity and dispersion of the residuals using the *DHARMa* package (Hartig, 2020).

3. Results

3.1. Prevalence of abnormal behaviours

Of the 28 abnormal behaviours included in the ethogram from the literature on chimpanzees, only 13 were observed in bonobos. The behaviours *Auto-aggression, Cling, Ear cover, Eye poke, Genital pat, Head bang, Pace, Raspberry vocalisation, Repetitive body movement, Self-mutilation, Self-slap, Spit, Stick out tongue, Suck self* and *Throw* were not recorded. Each of the 51 observed bonobos in our study engaged in abnormal behaviours since all of them performed *Coprophagy*, which was therefore the most prevalent behaviour. The other most prevalent abnormal behaviour we recorded were *Poke anus* (66.7%), *Social hair pluck* (51.0%), *Regurgitate* (49.0%) and *Head shake* (39.2%) (Figure 1).

3.2. Diversity of abnormal behaviour

The individual diversity ranged from 1-8 abnormal behaviours with a median of 4 abnormal behaviours per individual and was significantly influenced by rearing history ($\chi^2 = 6.478$, df = 2, $P = 0.039$). Specifically, wild-born individuals showed a significantly higher diversity (mean = 3.739, SE = 0.303) compared to mother-reared individuals (mean = 2.889, SE = 0.172; $t(74) = -2.039$, $P = 0.045$), see Figure 2a. Hand-reared individuals had a similar pattern, with a higher abnormal behavioural diversity (mean = 3.727, SE = 0.574) than mother-reared individuals (mean = 2.889, SE = 0.172), but the difference was not significant ($t(74) = -1.937$, $P = 0.057$).

3.3. Frequency of abnormal behaviours

Looking at the frequencies of abnormal behaviours, there was a large inter-individual variation ranging from 0.302 to 15.322 events/hour, with a median of 1.781 events/hour. Variation in the overall frequency of abnormal behaviours could not be explained by any of the predictors (age, sex, rearing history or the personality traits Activity, Boldness, Openness and Sociability).

Rearing history did predict the frequency of *Poke Anus* (χ^2 = 9.780, df = 2, *P* = 0.008) with wild-born individuals (mean = 0.537, SE = 0.147; *t*(71) = -2.737, P = 0.008) and hand-reared individuals (mean = 0.228, SE = 0.126; *t*(71) = -2.113, P = 0.038) showing this behaviour more frequently than mother-reared individuals (mean = 0.093, SE = 0.028; Figure 2b). *Poke Anus* was also significantly different between sexes, (χ^2 = 7.411, df = 1, *P* = 0.006) with females (mean = 0.344, SE = 0.079) showing higher frequencies than males (mean = 0.082, SE = 0.045), see Figure 2c.

Sociability predicted the frequency of *Coprophagy* (χ^2 = 15.073, df = 1, *P* < 0.001) and *Social hair pluck* (χ^2 = 4.884, df = 1, *P* = 0.027). Individuals scoring high on Sociability showed lower frequencies of *Coprophagy* (β = -0.496, SE = 0.128, Figure 3a), but higher frequencies of *Social hair pluck* (β = 0.807, SE = 0.365, Figure 3b).

Lastly, Activity scores predicted the frequency of *Coprophagy* (χ^2 = 8.253, df = 1, *P* = 0.004) and *Head shake* (χ^2 = 9.322, df = 1, *P* = 0.002). Individuals scoring high on Activity had lower frequencies of *Coprophagy* (β = -0.332, SE = 0.116, Figure 3c) and lower frequencies of *Head shake* (β = -1.300, SE = 0.426, Figure 3d). Fixed effects tables for all the GLMMs described in the main text are provided in tables in Table S2 and S3.

4. Discussion

We studied the abnormal behaviour in zoo-housed bonobos and investigated which factors were related to their occurrence. Variation in the diversity and frequency of individual behaviours could be explained by the individual's rearing-history, sex and/or personality traits.

Of the 28 abnormal behaviours included in the ethogram, we observed 13 behaviours in the 51 bonobos included in the study. This is lower than the 37 abnormal behaviours previously reported in a study with 40 zoo-housed chimpanzees with similar data collection methods (Birkett and Newton-Fisher, 2011). Similar to other chimpanzee studies (Birkett and Newton-Fisher, 2011; Jacobson et al., 2016; Martin, 2002; Nash et al., 1999, but see Bloomsmith et al., 2019), we found *Coprophagy* to be the most prevalent abnormal behaviour, as all bonobos exhibited this behaviour.

On average, bonobos showed 4 abnormal behaviours, performing them 1.78 times per hour. While this number seems high and corresponds to a similar study on chimpanzees (Birkett and Newton-Fisher, 2011), there is the possibility that our data represent an overestimation (Ross and Bloomsmith, 2011). Namely, it is important to acknowledge that for many of the abnormal behaviours, there is currently no clear link to their origin or their effect on animal welfare. To avoid such generalisation, it can be helpful to consider four ways abnormal behaviours can relate to welfare (Cooper and Mason, 1998): as an indicator of poor welfare; an adaptation to captivity; the physical harm of the behaviour; or the behaviour does not have a large direct impact on the quality of life. For example, *Coprophagy* is increasingly questioned as an indicator of negative welfare (Hopper et al., 2016) as accumulating studies suggest that it may be socially learnt (Freeman and Ross, 2014; Jacobson et al., 2016; Nash et al., 1999). *Coprophagy* is also observed in multiple wild bonobo populations (Beaune et al., 2017; Goldstone et al., 2016; Sakamaki, 2010) where it may be an adaptive feeding strategy when food is scarce (Sakamaki, 2010) and a cultural behaviour in some populations to cope with high tannin levels of *Canarium* fruits (Beaune et al., 2017).

Social learning may also play a role in the acquisition of other abnormal behaviours. *Social hair pluck* may be socially learnt as this behaviour is embedded in grooming activities (Brand and Marchant, 2019). Our data provide extra support for social learning of *Social hair pluck*, as it was present in four of the six surveyed locations. Instances of social transmission are also reported for *Regurgitation* in chimpanzees (Kalcher-Sommersguter et al., 2013) and bonobos (Stevens and Wind, 2011) and for *Poke anus* in bonobos (Stevens and Staes, unpublished data). Nonetheless, even if social learning, rather than past or present stressors, explains why individuals acquire certain abnormal behaviours, this does not exclude health implications (Cooper and Mason, 1998) and a potential impact on animal welfare. For example, *Regurgitation* (often followed by reingestion) has health consequences for the throat and teeth (Hill, 2009), *Coprophagy* may contribute to parasitic and bacterial disease transmission (Graczyk and Cranfield, 2003), and hair loss due to hair plucking (either self-directed or social) could interfere with homeothermy (Mcfarland et al., 2016). Even when such abnormal behaviours are not directly linked to suboptimal (social) environments and thus are not indicators of impaired psychological wellbeing, they can affect the health of an animal, and therefore negatively impact their welfare (Cooper and Mason, 1998).

When looking at the factors influencing abnormal behaviours in bonobos, we found that the absence of maternal care was linked to a higher diversity of abnormal behaviours, as well as to higher frequencies of *Poke anus*. This corroborates other studies reporting a higher diversity of abnormal behaviours in socially deprived chimpanzees (Martin, 2002), as well as a higher occurrence of abnormal behaviour in non-mother reared chimpanzees (but not for *Coprophagy* (Jacobson et al., 2016)). The exact history of the wild-born apes is often unknown, and their experience may vary from being ex-pets to passing through animal dealers. Yet, anecdotal reports suggest that many of these individuals were separated from their mother at an early age and were often deprived of social contact with their peers, resulting in the development of more abnormal behaviours (Martin, 2002) which may persist throughout life (Bloomsmith et al., 2019; Kalcher-Sommersguter et al., 2013). The bonobo breeding program has encouraged mother rearing since the 1990s and the import of wild-caught individuals has been stopped in the 1980s, with only few confiscated individuals from private persons entering the zoo population. Therefore, wild-caught and hand-reared individuals largely represent past practice and the latter only happens in life-threatening situations.

Sex effects are repeatedly observed for abnormal behaviours but often vary between behaviours and species (Bloomsmith et al., 2019; Lutz, 2018). We only found a sex effect for the frequency of *Poke anus*, such that females performed this behaviour more frequently than males. While the occurrence of *Poke anus* may be explained by social learning (Stevens and Staes, unpublished data), our observation that females performed this behaviour more often suggests that other mechanisms contribute to the expression of this behaviour, possibly self-stimulation (Vasey and Duckworth, 2006), but this remains to be studied.

We provide additional evidence that personality is linked to abnormal behaviours (Cussen and Mench, 2015; Gottlieb et al., 2013; Schork et al., 2018). Bonobos with lower Activity scores engaged more frequently in *Coprophagy* and *Head shake*. Lower Activity scores are characterised by lower levels of activity and higher levels of self-scratching (Staes et al., 2016). Increased rates of abnormal behaviour, mainly coprophagy in chimpanzees (Bloomsmith and Lambeth, 1995), have been observed in primates before predictable feeding times and were associated with heightened levels of inactivity (Bloomsmith and Lambeth, 1995; Waitt and Buchanan-Smith, 2001), while other studies in contrast report increased food-anticipating activity before feeding moments (Krebs et al., 2017). Taking this into consideration with the findings of our study, it is possible that *Coprophagy* is linked to feeding moments and that less active bonobos perform this behaviour more within these contexts. To better understand *Coprophagy* in bonobos, future research could focus on when exactly this behaviour is performed, and whether it is linked to feeding moments. We also found that less active bonobos showed higher frequencies of *Head shake*. Head shaking behaviour was initially considered an abnormal behaviour (Walsh et al., 1982), but recent studies suggest that this behaviour functions as a communicative gesture for initiating or resuming interactions such as play (Pika et al., 2005) or to prevent group members from engaging in a particular behaviour (Schneider et al., 2010). At this stage, it is unclear why less active individuals showed higher rates of *Head shake* and future research could focus on possible associations between the use of communicative gestures and personality profiles.

Interestingly, more sociable bonobos engaged less frequently in *Coprophagy*. This result seems contradictory to previous studies suggesting that higher sociability (e.g. mother-rearing conditions) facilitate the acquisition of *Coprophagy* through social learning (Freeman and Ross, 2014; Jacobson et al., 2016; Nash et al., 1999). However, it is important to note that we addressed the frequency of *Coprophagy* and not its prevalence. Higher Sociability scores are characterised by more frequent grooming bouts, more neighbours and higher grooming diversities, suggesting that these bonobos have richer social lives while less sociable individuals have fewer positive social interactions (Staes et al., 2016). Less sociable individuals may experience some form of boredom as sociability is considered a pillar contributing to primate welfare (Robinson et al., 2017). Boredom is previously used to explain *Coprophagy* in captive apes (Hoff et al., 1994; Martin, 2002) which could also explain why less sociable individuals engaged more in *Coprophagy*.

More sociable bonobos also performed more *Social hair pluck*. *Social hair pluck* is embedded in grooming activities of bonobos (Brand and Marchant, 2019), which may explain the positive association between Sociability scores and the frequency of *Social hair pluck*. Bonobos have several social grooming cultures (van Leeuwen et al., 2020) and social hair plucking may be a part of their cultural behaviour in captivity. Although *Social hair pluck* is not related to urinary cortisol levels (Brand et al., 2016), it is currently unclear if it is an appropriate indicator of poor welfare as individuals showing abnormal behaviour within a given environment likely have better welfare than those that do not perform these behaviours (Mason and Latham, 2004). More research is needed to understand how *Social hair pluck* influences bonobo welfare.

5. Conclusion

All bonobos performed at least one behaviour that is traditionally considered as abnormal. Yet, prevalent behaviours, such as *Coprophagy*, *Poke anus*, *Regurgitation* and *Social hair pluck*, may be acquired through social learning and hence cannot unconditionally be used as welfare indicators, although potential health implications must also be assessed. Variation in the frequency of single abnormal behaviours was observed and can partly be explained by rearing history, sex and/or personality traits. We were able to sample a relatively large number of bonobos, although future studies should aim to increase the sample size even further to look at possible interactions effects between risk factors which can reveal patterns that will further increase our understanding of abnormal behaviours in this species.

Altogether, the results of this study have several implications for the welfare of zoo-living bonobos. First, mother rearing is the most optimal condition in which bonobos can be raised and we encourage the bonobo breeding program to keep this as the standard. Second, social learning of abnormal behaviours complicates the elimination of behaviours such as *Coprophagy*, *Poke anus*, *Regurgitation*, and *Social hair pluck* from the zoo population, especially as they appear to be rather widespread. Still, zoos can attempt to mitigate abnormal appetitive behaviours including *Coprophagy* and *Regurgitation* through dietary manipulations and behavioural enrichment programs, which can be tailored to the personality profiles of the bonobos. Mitigating *Social hair pluck* may be more challenging as it is embedded in grooming activities, which are considered a positive behaviour. Two bonobo groups in our sample did not perform *Social hair pluck* at all and, in theory, one could prevent social transmission of this behaviour by not introducing individuals that engage in *Social hair pluck*. However, from a practical point of view, transfers between zoos are crucial to retain a viable breeding population and isolating the non-performing groups would therefore not be recommended.

Lastly, we suggest that future studies focus on how specific abnormal behaviour impact the psychological welfare of an individual. For example, cognitive bias testing revealed that head twirls, but not pacing, was an accurate indicator of negative emotional states in tufted capuchins (*Sapajus apella*) (Pomerantz et al., 2012). In the future, cognitive bias testing can also help to identify risk factors for the psychological welfare of individuals, including personality (Asher et al., 2016; Cussen and Mench, 2014). In conclusion, this study gives a starting point for a better understanding of why some individuals show more abnormal behaviours than others. These findings can contribute to a better understanding of abnormal behaviours in zoo-housed bonobos from which the captive care and management for the species can be further optimised.

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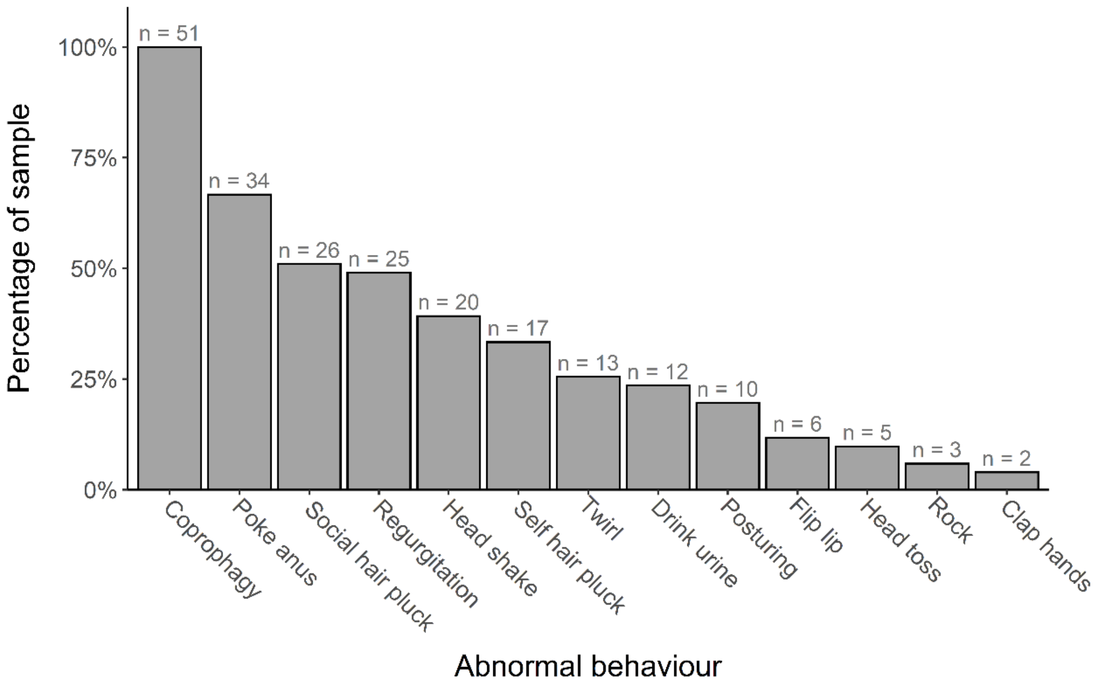
Figure captions

Figure 1: Percentage of the bonobos in the sample observed to perform each individual abnormal behaviour at least once during the period of observation.

Figure 2: Median diversity of abnormal behaviour based on the (a) rearing history and median frequency of Poke anus based on the (b) rearing history and (c) sex. *$P < 0.05$ and ** $P < 0.01$.

Figure 3: The association between the personality score Sociability and the frequency of (a) Coprophagy and (b) Social hair pluck and the personality score Activity and the frequency of (c) Coprophagy and (d) Head shake with the corresponding confidence intervals.



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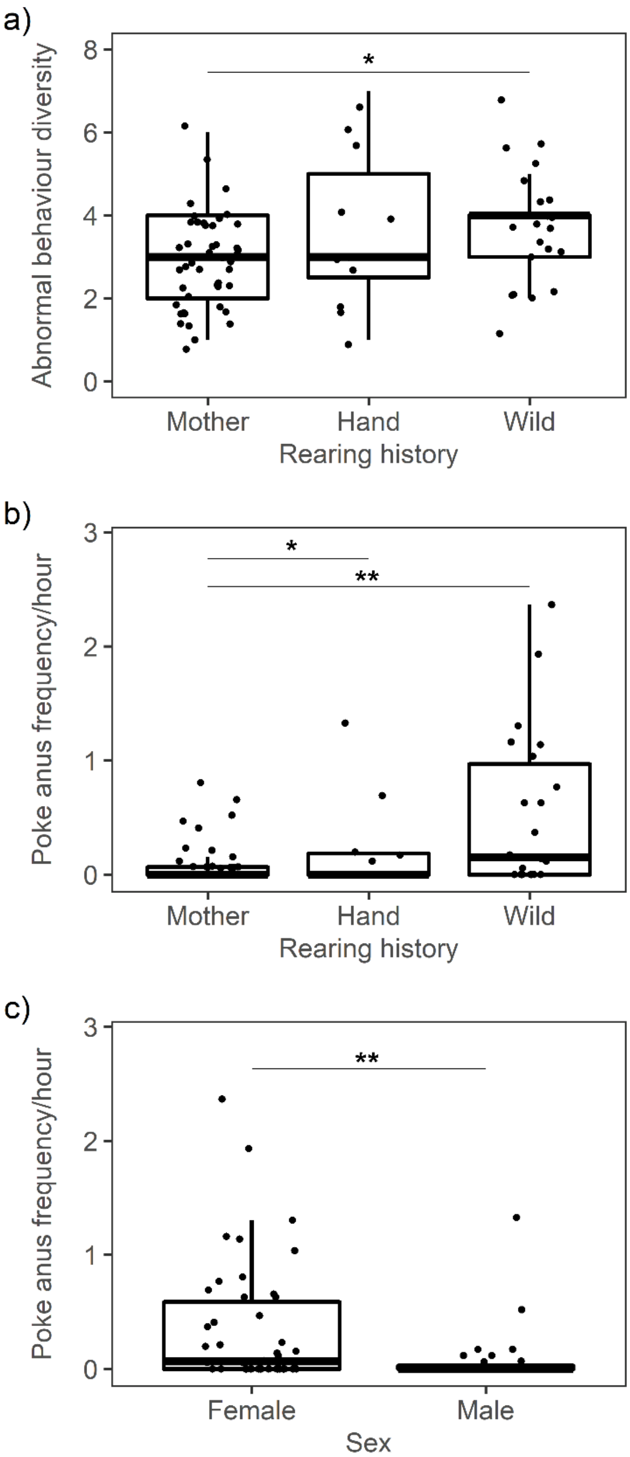

Figure 2: Median diversity of abnormal behaviour based on the (a) rearing history and median frequency of *Finger in anus* based on the (b) rearing history and (c) sex. *$P < 0.05$ and ** $P < 0.01$.

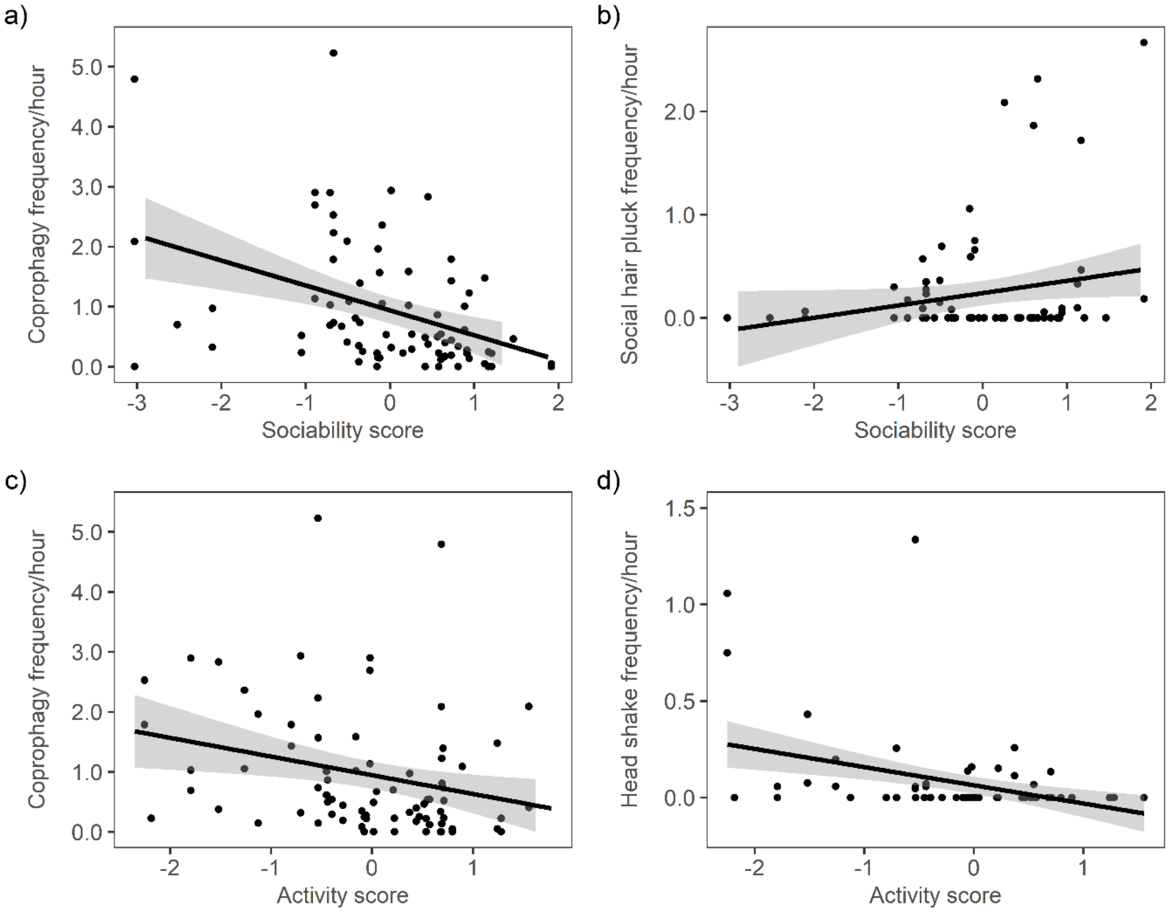

Figure 3: The association between the personality score Sociability and the frequency of (a) Coprophagy and (b) Social hair pluck and the personality score Activity and the frequency of (c) Coprophagy and (d) Head shake with the corresponding confidence intervals.

Electronic supplementary material

The influence of sex, rearing history, and personality on abnormal behaviour in zoo-housed bonobos (*Pan paniscus*)

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Table S1 – Variable loadings dimension reduction personality model (from Staes et al., 2016)

	Factor				
Variable	Sociability	Openness	Boldness	Activity	*h²*
Grooming Received	**0.83**	-0.03	-0.03	0.20	0.74
Grooming Density Received	**0.76**	-0.07	-0.12	0.14	0.68
Number of Neighbors	**0.71**	0.13	0.13	-0.04	0.54
Grooming Given	**0.67**	0.18	0.13	0.39	0.69
Latency to Approach Puzzle	**-0.66**	**-0.49**	0.02	0.24	0.79
Grooming Density Given	**0.64**	0.20	0.33	**0.42**	0.84
Latency to Approach Durian	**-0.64**	-0.23	-0.01	0.14	0.47
Grooming Diversity Index	**0.53**	0.12	0.19	0.36	0.67
Autogroom	**-0.48**	0.10	-0.39	0.01	0.46
Puzzle Number of Approaches	0.08	**0.91**	0.13	0.06	0.83
Play	-0.07	**0.70**	0.00	0.22	0.63
Time in Proximity to Puzzle	0.20	**0.68**	-0.31	0.03	0.59
Approach others	0.05	**0.65**	0.35	0.27	0.69
Taste Pasta	0.27	**0.41**	0.20	0.11	0.42
Leopard Number of Approaches	0.02	0.11	**0.82**	0.02	0.67
Leopard Number of Displays	0.21	0.07	**0.62**	-0.01	0.48
Time in Proximity to Leopard	0.10	-0.08	**0.59**	**-0.44**	0.54
Aggression Received	-0.37	0.12	**0.54**	0.31	0.54
Self-scratch	-0.10	-0.17	0.19	**-0.69**	0.66
Activity	0.29	0.30	0.26	**0.53**	0.65
Eigenvalue	5.98	2.85	2.59	1.73	
% variance explained	29.92	14.25	12.93	8.65	

Boldface indicates loadings >|0.40|

Table S2: Fixed effects for the diversity of abnormal behaviour.

Predictors	*Estimates*	*std. Error*	*z value*	*p*
Diversity				
(Intercept)	-1.35	0.10	-14.12	**<0.001**
Rearing [*Hand*]	0.43	0.22	1.94	0.053
Rearing [*Wild*]	0.38	0.19	2.04	**0.042**

Reference category for Rearing was set to Mother-reared.

Table S3: Fixed effects for the frequency of individual abnormal behaviours.

Predictors	*Estimates*	*std. Error*	*z value*	*p*
All				
(Intercept)	0.885	0.157	5.625	**<0.001**
Coprophagy				
(Intercept)	-0.215	0.116	-1.858	0.063
Activity score	-0.332	0.116	-2.873	**0.004**
Sociability score	-0.496	0.128	-3.882	**<0.001**
Finger in anus				
(Intercept)	-2.215	0.474	-4.674	**<0.001**
Sex [*Male*]	-1.627	0.598	-2.722	**0.006**
Rearing [*Hand*]	1.655	0.783	2.113	**0.035**
Rearing [*Wild*]	1.720	0.628	2.737	**0.006**
Social hair pluck				
(Intercept)	-1.482	0.287	-5.167	**<0.001**
Sociability score	0.807	0.365	2.210	**0.027**
Regurgitation				
(Intercept)	-0.196	0.373	-0.526	0.599
Head shaking				
(Intercept)	-4.372	0.752	-5.815	**<0.001**
Activity score	-1.300	0.426	-3.053	**0.002**

Reference category for Sex was set to Female and for Rearing to Mother-reared.