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The Old School, Brewhouse Hill, Wheathampstead,
Hertfordshire AL4 8AN, UK
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Individual variation in chimpanzee (Pan troglodytes) *repertoires of abnormal behaviour*

Z Goldsborough[*†‡§], EHM Sterck[†#], FBM de Waal[†¥] and CE Webb[†¶]*

[†] Animal Behaviour & Cognition, Department of Biology, Utrecht University, Utrecht, The Netherlands
[‡] Department for the Ecology of Animal Societies, Max Planck of Animal Behavior, Bücklestraße 5a, Room 519a, 78467, Konstanz, Germany
[§] Department of Biology, University of Konstanz, Konstanz, Germany
[#] Animal Science Department, BPRC, Rijswijk, The Netherlands
[¥] Department of Psychology, Emory University, Atlanta, USA
[¶] Department of Human Evolutionary Biology, Harvard University, Cambridge, USA
* Contact for correspondence: zgoldsborough@outlook.com

Abstract

Abnormal behaviour in captive animals is both pervasive and ambiguous. Although individual differences are central to the field of animal welfare, studies on abnormal behaviour predominantly employ quantitative, population-level approaches. For example, whereas previous studies on chimpanzee (Pan troglodytes) *abnormal behaviour have reported significant variation between groups or individuals in the quantity (eg frequency and duration) of abnormal behaviour, much less is known about qualitative differences. Individual abnormal behavioural repertoires may be highly idiosyncratic, where certain behaviours are over-represented (ie individually specific abnormal behavioural 'signatures'). The present study investigated qualitative individual variation in the abnormal behaviour of chimpanzees (n = 15) housed at Royal Burgers' Zoo in Arnhem, The Netherlands. Substantial variation was found between individuals in the diversity (size and evenness) and overall composition of their abnormal behavioural repertoires. Factors including age, sex, and rank did not significantly account for dissimilarity of individuals' abnormal behavioural repertoires, but kin dyads showed more similar abnormal behaviour than non-kin dyads. Further exploratory analyses examined whether individual variation in one abnormal behaviour (coprophagy) predicted variation in stress-related behaviour (self-scratching). This allowed us to tentatively conclude that there were also individual differences in the link between a given abnormal behaviour and the behavioural expression of stress. Qualitative individual variation in abnormal behaviour provides a novel angle to a literature traditionally focused on quantifying abnormal behaviour at the group- or species-level and may thus represent an important yet previously overlooked source of variation in the extent to which abnormal behaviour reflects the state of individual welfare.*

Keywords: *animal welfare, chimpanzees, coprophagy, stereotypical behaviour, stress, zoo-housed*

Introduction

Many animals in zoos and other captive settings exhibit behaviour unlike that of their wild counterparts. These 'abnormal behaviours' have been defined as differing in either quantity or quality from the behaviour of wild animals (Erwin & Deni 1979). Perhaps implied by the term itself rather than by definition, abnormal behaviour is commonly presumed to be an indicator of a poor welfare state (Mason 2006). In support of this, impoverished physical or social housing are linked to higher rates of abnormal behaviour (Bloomsmith *et al* 2006; Greening 2019). However, not all studies report a clear link between abnormal behaviour and compromised welfare (Jacobson *et al* 2016; Clay *et al* 2018).

Recent animal welfare initiatives have highlighted the experience of the individual and individual differences in assessing welfare (Marchant-Forde 2015; Brando & Buchanan-Smith 2018). In contrast, prior studies on the occurrence of abnormal behaviour are typically conducted at the group- (Lutz 2018) or even species-level (Mason 2006; Birkett & Newton-Fisher 2011; Jacobson *et al* 2016; Clay *et al* 2018; Bloomsmith *et al* 2019), thus documenting variation in abnormal behavioural repertoires at the 'super-individual' level of analysis. On the rarer occasion that individual differences in abnormal behaviour are emphasised, a focus on *quantity* (the frequency or duration of abnormal behaviour) has overshadowed systematic investigation on variation in the *quality* of abnormal behaviours (the type of abnormal behaviour) (Rose *et al* 2017).

Chimpanzees (*Pan troglodytes*) are a species in which abnormal behaviour has been well-documented, yet knowledge is very limited concerning individual differences in the quality of abnormal behavioural repertoires. Although most captive chimpanzees who show abnormal behaviour exhibit more than one type (Birkett & Newton-Fisher 2011; Bloomsmith *et al* 2019), each of these behaviours is generally analysed in isolation from other behaviours (Clay *et al* 2018; Bloomsmith *et al* 2019), or collapsed into one category of 'abnormal behaviour' (Yamanashi *et al* 2018; Neal Webb *et al* 2019), thereby overlooking qualitative aspects of abnormal behaviour — such as how each abnormal behaviour is embedded in the full abnormal behavioural repertoire of an individual.

Variation between individuals in abnormal behavioural repertoires may, in part, reflect factors that are known to affect the development of such behaviour, including age (Trollope 1977; Lutz *et al* 2003), sex (Trollope 1977; Jacobson *et al* 2016; Clay *et al* 2018; Bloomsmith *et al* 2019), and physical and social housing conditions, especially during rearing (Spijkerman *et al* 1994; Jacobson *et al* 2016). Nonetheless, even when accounting for these factors, chimpanzees show substantial individual variation in the quantity of abnormal behaviours they exhibit (Paulk *et al* 1977; Birkett & Newton-Fisher 2011). Birkett and Newton-Fisher (2011) reported the mean number of different abnormal behaviours shown by each subject and the proportion of subjects exhibiting a given behaviour but did not explicitly examine the abnormal behavioural repertoire of each individual relative to others. Additionally, certain abnormal behaviours are thought to spread via social learning (Jacobson *et al* 2016), implicating factors such as kinship and rank (Bonnie *et al* 2007; Hopper *et al* 2011; Schlingloff & Moore 2017). Echoing broader debates about the extent to which chimpanzee behaviours deemed 'abnormal' are genuine manifestations of stress or psychological suffering (eg Ross & Bloomsmith 2011 *cf* Birkett & Newton-Fisher 2011), it has further been argued that over time, an abnormal behaviour could be reduced to a habit that is no longer linked to the harmful context during which it developed (Fritz *et al* 1992; Mason & Latham 2004). The presence of individual variation and different causations for the development of abnormal behaviour only further calls into question the explanatory power and utility of group- or species-wide signatures of abnormal behaviour as a measure of welfare. Moreover, it highlights the importance of understanding the individual's abnormal behavioural repertoire in order to more accurately assess the state of that individual's welfare.

Recent research on coprophagy seems to exemplify this issue by suggesting that the link between this abnormal behaviour and its welfare implications can be ambiguous. Coprophagy, the consumption of one's own faeces (*cf* Hopper *et al* 2016), is the most common and well-studied abnormal behaviour in chimpanzees (Birkett & Newton-Fisher 2011). While not entirely absent in wild-living chimpanzees, coprophagy is much more abundant in captivity (Hopper *et al* 2016). Already in the 1960s, it was suggested that coprophagy in chimpanzees and other captive primates could be linked to stress, boredom, and other signs of poor welfare (Hill 1966). This notion has only been reinforced by more recent studies that conceptualise coprophagy as an undesirable and theoretically negative abnormal behaviour (Nash *et al* 1999; Hook *et al* 2002; Birkett & Newton-Fisher 2011; Jacobson *et al* 2016). However, in some groups of captive chimpanzees, there is evidence that coprophagy is socially learned (Bloomsmith *et al* 2006; Jacobson *et al* 2016), and perhaps not predictive of poor welfare at all (Hopper *et al* 2016). For example, coprophagy may be a foraging strategy: a tactic to obtain nutrients from hard to digest seeds by ingesting them a second time (Fritz *et al* 1992; Krief *et al* 2004; Payne *et al* 2008; Bertolani & Pruetz 2011). As such, despite the prevalence of coprophagy in captive chimpanzee populations, there is no consensus over whether it is a reliable indicator of a poor welfare state. Notwithstanding these ambiguities, if individuals reliably vary in their abnormal behavioural repertoire, it follows that such variation may also be apparent in the abnormal behaviours that are linked to behavioural signals of stress. In this case, the inconsistencies in the current literature (such as when it comes to the link between coprophagy and stress) may, in part, be ameliorated by a more individual-focused approach to abnormal behaviour, which could in turn yield more accurate welfare assessments than do conventional, group-wide methods.

Relative to abnormal behaviours, evidence for a link between self-directed behaviours, like self-scratching, and individual stress is well-documented. There is convincing physiological and pharmacological evidence in non-human primates that self-scratching is a behavioural manifestation of short-term stress (Maestripieri *et al* 1992; Schino *et al* 1996; Whitten *et al* 1998). For example, self-scratching has been observed to increase in chimpanzees in stressful situations, such as immediately after a conflict (Leavens *et al* 2004; Koski & Sterck 2007), and to decrease after consolation (Fraser *et al* 2008). Additionally, administering anxiogenic drugs to non-human primates leads to an increase in both circulating cortisol and self-scratching (Ninan *et al* 1982; Crawley *et al* 1985), while anxiolytic drug administration results in a decrease in both (Schino *et al* 1991). Thus, in this study, we consider elevated rates of self-scratching as one indicator of an individual's poor welfare state.

The primary aim of this study is to systematically assess individual variation in the quality of individual abnormal behavioural repertoires of captive chimpanzees by employing two novel methods that test abnormal behaviour diversity and the dissimilarity of repertoires between individuals. As a secondary aim, we explore potential factors that could explain such variation. Lastly, we consider whether the link between abnormal behaviour (coprophagy) and stress (assessed via self-scratching behaviour) may also be subject to, and therefore partially explained by, individual variation.

Materials and methods

Ethical approval

This study involved non-human animals but was purely observational in nature, meaning that no invasive procedures were conducted. Permission to conduct this study was granted by Royal Burgers' Zoo, Arnhem, The Netherlands.

Study animals and housing

Subjects were 15 adult chimpanzees socially housed at Royal Burgers' Zoo in Arnhem, The Netherlands (Table 1). During the study period, the colony comprised four males and eleven females, two of whom were added to the colony on the 12th of February 2016 as part of the European Endangered Species Programme (EEP) from the European Association of Zoos and Aquaria (EAZA).

The chimpanzees typically had access to either an indoor (± 386 m^2) or outdoor enclosure (± 7,000 m^2), and, at times, could move freely between the two. The outdoor enclosure was semi-natural, consisting of vegetation such as bushes, trees and grass, several climbing structures, and a surrounding moat. The indoor enclosure was furnished with wooden platforms, ropes, nets, and barrels, along with loose objects such as towels, balls, and buckets. At night, the chimpanzees were kept in the inside enclosure. The chimpanzees received food three times a day, at around 0900, 1230 and 1600h, and had access to water *ad libitum*.

Table 1 Subject demographics as of 1st June 2018.

Individual	Sex	Age	Rank	Maternal kinship
Giambo	M	29	High$^{\alpha}$	
Jing	M	37	High$^{\beta}$	Jimmie (mother)
Ghineau	M	13	High	Gaby (mother)
Fons	M	43	High	
Raimee	F	19	High	Roosje (mother)
Roosje	F	39	High	Raimee (daughter)
Morami	F	31	Medium	Moniek (mother)
Tushi	F	26	Medium	
Gaby	F	34	Medium	Ghineau (son)
Moniek	F	41	Medium	Morami (daughter)
Geisha	F	25	Medium	
Erika*	F	26	Medium	
Jimmie	F	58	Low	Jing (son)
Moni*	F	29	Low	
Tesua	F	32	Low	

$^{\alpha}$ Alpha male;
$^{\beta}$ Beta male;
* Recently introduced.

Data collection

Data collection took place between 20th November 2017 and 1st June 2018, during which observations were conducted approximately four times per week between 0900 and 1700h. Behavioural observations were recorded in the Time Stamped Fieldnotes programme (Neukadye 2017) using an iPad.

We conducted 10-min focal observations per individual per day to document individual abnormal behavioural repertoires (Martin & Bateson 2007). Nine abnormal behaviours (Table 2) were selected *a posteriori* on the basis of two criteria: their reliable presence in the colony (ie performed on multiple occasions by at least three individuals), and their inclusion in previous literature on abnormal behaviour in captive chimpanzee populations (Walsh *et al* 1982; Birkett & Newton-Fisher 2011; Hopper *et al* 2016). One additional abnormal behaviour was observed in this group, namely the crossed-arm walk, which was included here as a locomotive version of the more commonly described body-manipulation or persistent body movement. Furthermore, several abnormal behaviours were included in the initial ethogram, but were not analysed as they were either not observed (in the case of auto-mutilation, self-clasping, pacing, regurgitation-reingestion, and twirl), hard to observe reliably (fumbling of the nipple) or ambiguous in function (body-shake, as it is also related to cold weather), (for definitions, see Birkett & Newton-Fisher 2011).

The order of focal subjects was obtained via randomisation, and the focal samples were balanced across the day and the observers. All observations involved two concurrently trained observers who demonstrated inter-rater reliability scores > 75% for all observational protocols and corresponding behaviours before data collection began. Data were always collected as a pair, with one individual observing while the other entered data on the iPad. Focal observations were only included if the subject was visible for > 75% of the observation. Focal observations took place before and after the daily global observation window (see below), and every individual was only sampled once per day. This yielded an average of ± 13 h of focal data per individual. Additionally, a 90-min global observation of the entire group was conducted daily (total ±119 h), during which we also recorded the occurrence of abnormal behaviours. Abnormal behavioural repertoire size and rate (respectively) in the global observations were correlated with those derived from the focal observations (Pair-wise Spearman's rank correlation, size: $r_s = 0.69$; $P = 0.004$, rate: $r_s = 0.93$; $P < 0.001$), ie individuals with the largest repertoire in the focals also showed the largest repertoire in the globals. However, some individuals were observed to perform additional abnormal behaviours in the global observations that were not recorded in the focal, and although we are confident that recorded abnormal behaviours were correct, these global group observations pose a higher risk of containing type II errors (failing to record more subtle abnormal behaviours). Therefore, we use the focal data for our main analyses on subjects' abnormal behavioural repertoires, as this provides more accurate estimates of rates, and include a frequency table of the abnormal behaviour in the global observations (Table S1; see supplementary material

Table 2 Ethogram of abnormal behaviours used in this study.

Behaviour	Definition	Source
Body manipulation	Manipulates specific area of the body in a repeated*, sustained and purposeless manner (eg eye-poking, self-patting or ear covering)	2
Clap	Slaps palm of hand or sole of foot, producing an audible sound (outside of feeding context)	3
Coprophagy	Deliberately ingests faeces of self or another individual	4
Head-shake	Rolls or shakes head in quick motion	4
Crossed-arm walk	Walks quadrupedally while holding one arm crossed in front of their body, can be empty-handed or carrying something	1
Manipulate faeces	Holds, carries or spreads own or other's faeces on surface**	3
Pluck	Pulls out own hair	3
Rock	Sways repetitively* and rhythmically, without piloerection	3
Urine interaction	Places hand or foot in own urine stream, may wipe hand on body after, or deliberately ingests urine from self or other	2, 4

* Repetitive is defined as having taken place at least three times;
** Faeces being held or carried while being ingested was scored as coprophagy.
[1] The current study; [2] Hopper *et al* (2016); [3] Walsh *et al* (1982); [4] Birkett & Newton-Fisher (2011).

to papers published in *Animal Welfare*: https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material).

In order to establish a dominance hierarchy, agonistic interactions were recorded *ad libitum* and dominance rank was quantified using Matman Excel® (de Vries *et al* 1993), based on a combination of submissive and agonistic behaviours (see Table A1: https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material). Due to inconsistencies in the linear hierarchy resulting from the agonistic data, individuals were categorised as 'high', 'medium' or 'low' ranking, based on the keepers' and observers' knowledge, resulting in the classification displayed in Table 1.

To assess whether the link between one abnormal behaviour and stress varies between individuals, we selected coprophagy — the most documented abnormal behaviour in chimpanzees and one of the most prevalent abnormal behaviours in the study colony. We used self-scratching as a behavioural indicator of stress (see Maestripieri *et al* 1992; Schino *et al* 1996; Whitten *et al* 1998), which was operationalised as 'dragging hands or feet across part of the body, either repeated or in long, rough strokes' (Baker & Aureli 1997; Kutsukake 2003; Koski & Sterck 2007).

Statistical analysis

First, we examined the presence of individual variation in the overall abnormal behavioural repertoire quantitatively, by determining an individual's hourly rate of abnormal behaviour, and qualitatively through diversity and dissimilarity indices. The hourly rate was calculated by dividing an individual's total number of abnormal behavioural occurrences across all observations by that individual's total number of focal hours. Diversity was assessed by considering both the overall size and degree of specialisation of an individual's abnormal behavioural repertoire, quantifying specialisation by means of an evenness score. An individual's abnormal behavioural repertoire size refers to the number of different abnormal behaviours it shows. The evenness score is a measure of the distribution of the repertoire, which was calculated by dividing H the Shannon-Weaver index, by the natural logarithm of the repertoire size, as proposed by Pielou (1966), and commonly used in ecology to assess species evenness or equitability. We used the rates of each abnormal behaviour shown by each individual to calculate H. The evenness score ranges between 0 and 1, with 1 indicating that every behaviour in the repertoire is represented equally, and numbers nearing 0 indicating the over-representation of certain behaviours over others.

Second, we quantified the dissimilarity in individuals' abnormal behavioural repertoires using a Euclidean distance matrix based on the rates of each abnormal behaviour. The Euclidean distance between two individuals was obtained by summing the differences between their rates for each abnormal behaviour. Before calculating the Euclidean distances, the behaviours were standardised to equalise their weight. Dissimilarity was calculated both on a dyadic level (ie, how dissimilar the repertoires of two individuals were to each other) and using an average 'dissimilarity score' per individual. The latter was obtained by taking the mean of each subject's Euclidean distance with every other member of the group. Since Euclidean distance measures dissimilarity, the higher the score is, the more dissimilar two individuals are. Therefore, the individuals with the lowest average dissimilarity score were most similar to the rest of the group in terms of their abnormal behavioural repertoire's composition.

Third, we tested other factors that could possibly account for individual variation in the diversity and dissimilarity of abnormal behavioural repertoires. For diversity scores and average dissimilarity scores, the effects of age, sex, and dominance rank were tested using standard parametric and non-parametric correlations, *t*-tests, and ANOVAs. Rearing history was not included as a predictor, since all individuals in the colony except two were mother-reared. Additionally, we considered the effect of each individual's average rate of abnormal behaviour on diversity and dissimilarity. For dyadic dissimilarity, we performed a Double Decker Semi-Partialling Multiple Regression Quadratic Assignment Procedure (MRQAP-DSP following Dekker *et al* 2007), to investigate if variation in dyadic dissimilarity could be predicted by differences in age, rank, sex, or by whether a dyad was kin or not. We ensured that the structure of our model and our data met the assumptions of the MRQAP-DSP test. Predictor matrices were constructed in the following ways. For age, we used the dyadic difference in age, and this matrix of age was row-centered as a way of standardisation to correct for its large standard deviation, ie the row mean was subtracted from each score in the row. For sex, we considered whether dyad members were of the same (0) or different (1) sex. A dyad's rank difference could be 0 (same rank), –1 (the individual is lower ranking than the other) or 1 (the individual is higher ranking than the other). Lastly, we considered dyadic matrilineal kinship, with 1 indicating that members were matrilineal kin (mother-offspring or full siblings) and 0 indicating that they were not. The dyadic dissimilarity matrix was also standardised via row-centering.

The MRQAP-DSP method tests whether one predictor matrix (such as age difference) is significantly associated with the dependent matrix (ie dissimilarity), while controlling for the effect of other predictor matrices. This approach accounts for non-independence of data (which is always present in network data as an individual appears in multiple dyads) by comparing the regression coefficients obtained from the observed data against a distribution of coefficients calculated from random permutations of the data. Double semi-partialing (DSP) makes this test robust and especially useful for network data like ours, consisting of continuous or skewed counts (Dekker *et al* 2007). We used the function mrqap.dsp from the R package 'asnipe' with 10,000 permutations (Farine 2013).

Lastly, as an exploratory analysis on individual variation in the relationship between coprophagy and stress, we initially considered this link at the group level in two ways: first, via a pair-wise correlation between the hourly rate of coprophagy and self-scratching over the entire observational period; second, via a pair-wise correlation between the number of occurrences of coprophagy per focal observation and the number of occurrences of self-scratching per focal observation. At the individual level of analysis, we conducted a pair-wise correlation between the number of instances of coprophagy and self-scratching per individual, using the focal observation as the unit of measurement. To control for the false discovery rate brought on by multiple testing, the Benjamini-Hochberg correction was used. We also examined other factors that could possibly account for individual variation in the link between coprophagy and self-scratching — namely age, sex, and dominance rank.

All analyses were conducted in R Studio (R Development Core Team 2016), with an alpha level of 0.05. Non-parametric tests were used when data were not normally distributed. The code and datasets used for analyses are available via https://doi.org/10.5281/zenodo.4748811.

Results

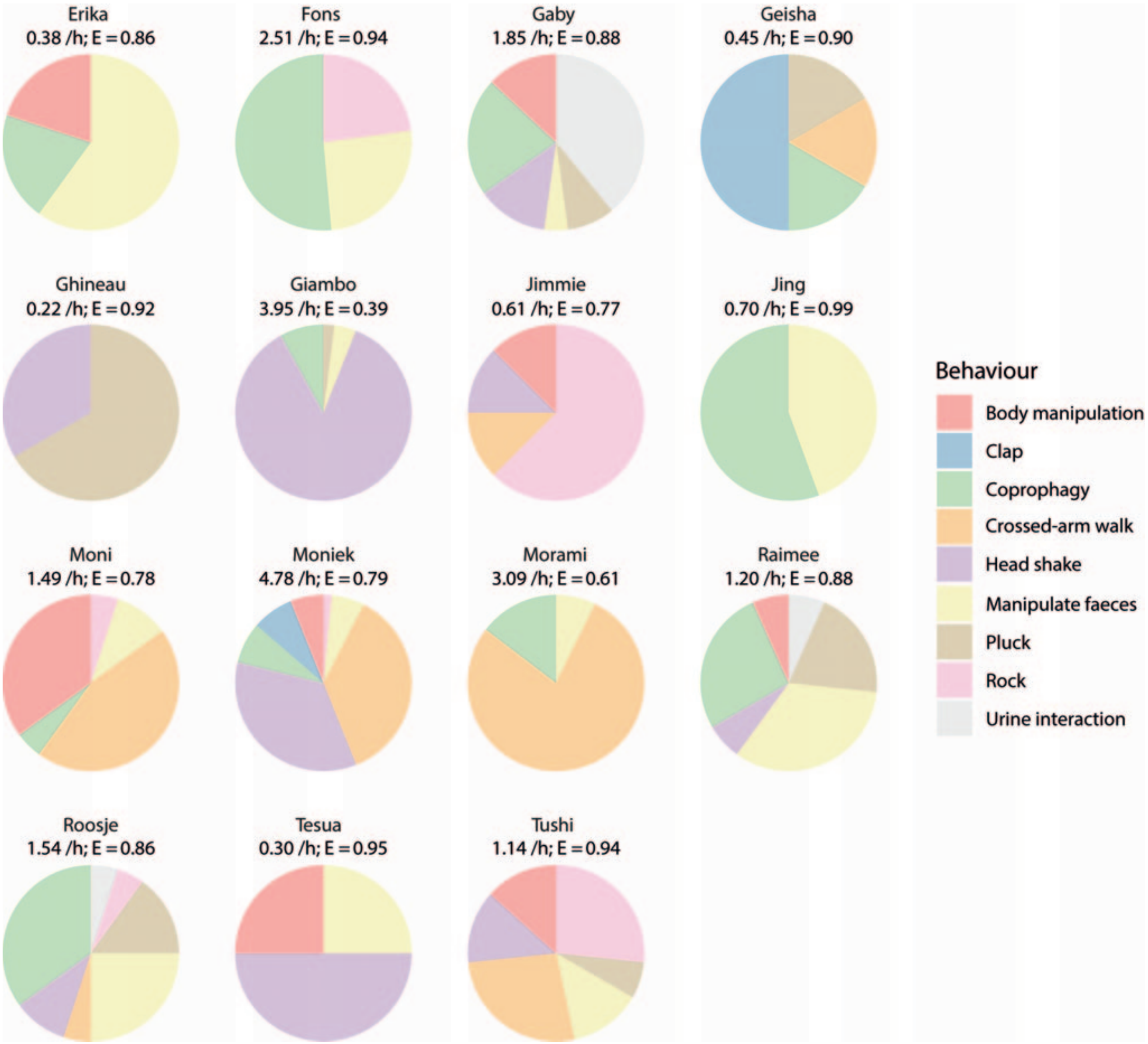
Diversity

A graphical overview of subjects' abnormal behavioural repertoires is provided in Figure 1. These individual abnormal behavioural signatures reveal unique repertoire compositions, exemplified by the fact that for the majority of subjects (nine out of 15), a single abnormal behaviour constituted ≥ 50% of the individual's repertoire. All subjects showed at least two abnormal behaviours, yet no individual showed all nine possible behaviours (median = 4; range 2–7). Nine individuals (60%) showed more than three unique abnormal behaviours. None of the observed abnormal behaviours occurred for every individual in the group, and manipulate-faeces and coprophagy were most common, observed in 12 and eleven individuals, respectively. When including the occurrence of abnormal behaviour in the global observations (Table S1; https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material), all 15 individuals showed coprophagy and manipulate-faeces. Again, no individual showed all nine abnormal behaviours, but all individuals had a larger repertoire size than in the focal data (median = 6, range = 4–8).

Females had significantly larger abnormal behavioural repertoires than males (Wilcoxon Rank Sum, $W_{RS} = 38.5$, $P = 0.033$, μ♀ = 5, μ♂ = 2.5). However, this difference seems to be due to the abnormal behaviour 'crossed-arm walk', which only females show; once this female-specific behaviour was excluded from analyses, no significant difference between male and female repertoire size was found. Neither age nor dominance rank were significant predictors of repertoire size. The mean (± SD) rate of abnormal behaviour was 1.54 (± 1.35) per hour (range 0.21–4.71). No significant relationship was found between the rate of abnormal behaviour and the size of the abnormal behavioural repertoire, nor any effect of sex, age, or rank on the abnormal behavioural rate.

The median evenness score was 0.88 (range 0.39–0.99), and the evenness score was not significantly correlated with repertoire size. Neither sex, age, nor rank significantly predicted evenness scores. However, individuals who showed a higher rate of abnormal behaviour had a significantly lower evenness score ($r_s = –0.53$; $P = 0.043$; Figure 2), indicating that they showed a more biased distribution than individuals with a lower rate of abnormal behaviour.

Figure 1



Each individual's abnormal behavioural repertoire, including the rate of total abnormal behaviour per hour and the evenness score E per individual.

Dissimilarity

The median average dissimilarity score between a given subject and the rest of the group was 3.75 (range 3.09–5.82). None of the predictors (age, sex, and dominance rank) accounted for differences in the average dissimilarity score. In regards to dyadic dissimilarity, including all four predictor matrices resulted in a significant model (MQRAP-DSP, $F_{4,206}$ = 7.18; P = < 0.001, R^2 = 0.11, Table S2; https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material). Matrilineal kinship was the only predictor significantly correlated with dissimilarity (B = –0.89; P = 0.016). This significant positive association indicates that kin dyads exhibited more similar abnormal behavioural repertoires (when controlling for sex, age, and rank) than non-kin dyads.

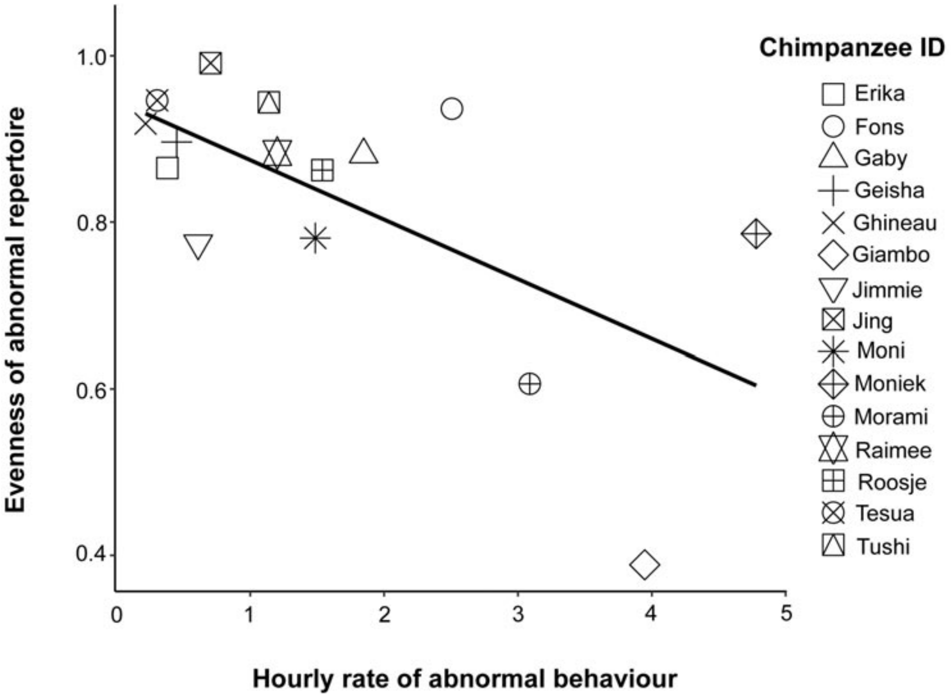
Coprophagy and stress

At the group-level, we found no significant correlation between the hourly rate of coprophagy and the hourly rate of self-scratching. At the individual-level, two subjects exhibited a significant positive correlation between the occurrence of coprophagy and self-scratching (Table S3; https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material).

Discussion

Individual variation in the abnormal behavioural repertoire of captive animals has received surprisingly limited attention. In this study, we demonstrate that chimpanzees differ substantially in the quality of their abnormal

Figure 2



Hourly rate of abnormal behaviour compared to evenness of abnormal repertoire with individuals as points and a line showing the smoothed conditional means.

behaviour, which further builds on previous research documenting quantitative individual differences in abnormal behaviour (Paulk *et al* 1977; Birkett & Newton-Fisher 2011). Individual abnormal behavioural repertoires were markedly dissimilar, and differences could not be explained by factors known to influence the development of abnormal behaviours, such as age and sex. These findings highlight the advantages of individual-based approaches to the study of abnormal behaviour, as opposed to identifying group- or species-specific patterns, which could in turn resolve inconsistencies in the literature when it comes to the association between abnormal behaviour and welfare.

Diversity

For the majority of individuals, one abnormal behaviour made up half or more of their repertoire, indicating the disproportionate expression of certain abnormal behaviours in individuals' repertoires. No single abnormal behaviour consistently made up the largest proportion of all subjects' repertoires, inviting us to speculate that individuals' repertoires were biased towards certain behaviours. Additionally, individuals with higher abnormal behaviour rates were found to have more biased repertoires than individuals who showed abnormal behaviour less frequently, further supporting that some individuals may have a tendency to frequently use a particular abnormal behaviour. This suggests the presence of individual specific abnormal behavioural signatures. It is unclear what may cause such individual biases in the expression of different abnormal behaviours. First, it is possible that the abnormal behaviours that an individual acquires earlier in their life become habitual and embedded and are thus exhibited more frequently than behaviours acquired later in life. However, we have no information on when our study subjects acquired certain abnormal behaviours. Alternatively, some abnormal behaviours may serve a specific function for an individual, such as reducing stress (see below). Identifying why individuals show a bias for a particular abnormal behaviour over others may shed light on the individually specific function of these behaviours, and thus poses an interesting avenue for future research.

Furthermore, the chimpanzees varied in the diversity of their abnormal repertoire, although factors other than individual identity played a role. In our group, contrary to some findings (Trollope 1977; Jacobson *et al* 2016), but in agreement with others (Marriner & Drickamer 1994; Birkett & Newton-Fisher 2011), we found no sex difference in the rate of abnormal behaviour shown. However, females had larger abnormal behaviour repertoires than males, an effect attributable to one behaviour, the crossed-arm walk, being female-specific. According to zoo-keeper records, this behaviour originated from one female over 20 years ago, and while other females have also shown this behaviour, males have never been observed to do so. Nonetheless, the female-specific nature of one of the included abnormal behaviours suggests that further research into sex differences in abnormal behaviour is warranted.

In contrast to previous studies (Trollope 1977; Lutz *et al* 2003), we found no significant effect of age on repertoire size or evenness. However, the effect of age on abnormal behaviours could differ per abnormal behaviour (Lutz *et al* 2003); thus, combining them into a single diversity measure may render age effects invisible. Additionally, the mean (± SD) age of the chimpanzees in the Royal Burgers' Zoo colony is high and shows little variance (32.1 [± 10.8]); the colony contains no juveniles nor infants, limiting the conclusions that can be drawn. Similarly, dominance rank did not have a significant effect on diversity indices. Moreover, individuals with large repertoire size were not more likely to show higher rates of abnormal behaviour, nor to have more evenly distributed repertoires than individuals who showed less different abnormal behaviours.

Dissimilarity

We found that kin dyads were more similar in their abnormal behavioural repertoire than non-kin dyads, potentially supporting the notion that abnormal behaviour can be socially learned (Jacobson *et al* 2016). Consistent with this notion, another study on this same population has suggested that the crossed-arm walk, one of the abnormal behaviours studied here, is socially learned (Goldsborough *et al* 2021). The dissimilarity of abnormal behavioural repertoires was not significantly affected by age, sex, or rank, neither when considering an individual's nor the dyads' averaged scores in the matrix regression. It is important to note however that our sample had limited variation in some predictors and thus low statistical power to detect significant differences. Future studies would ideally examine dissimilarity in abnormal behavioural repertoires with a more robust sample, also including further dyadic predictors such as affiliation strength which may partially account for the reported variation. For instance, rearing history has been shown to have a noteworthy effect on the occurrence of some abnormal behaviours (Spijkerman *et al* 1994; Clay *et al* 2018). The two hand-reared individuals in this colony did not have notable similarities in their abnormal behaviour repertoires, although both showed a relatively large number of different abnormal behaviours, which could be due to a number of other factors. As such, rearing history is a relevant factor to consider in future work on variation in the quality of abnormal behaviour. Chimpanzees are known for their cultural complexity (Whiten *et al* 1999; Boesch 2012), and thus future work should continue to examine the role of social learning in the acquisition and maintenance of individual abnormal behaviours.

Abnormal behaviour and stress

Abnormal behaviours are not necessarily linked to an impoverished welfare state (Mason 2006) and, moreover, the presence of such a link may vary per individual. At the level of the entire group, we found no overall link between coprophagy and self-scratching behaviour. However, at the level of the individual, we found a significant positive link between coprophagy and stress for some chimpanzees but not for others, indicating that the function of this abnormal behaviour may differ between individuals. It is important to note that the lack of a correlation between self-scratching and coprophagy for some individuals does not necessarily mean that the behaviour is positive for them. An abnormal behaviour could also be linked to boredom and a lack of stimulation, something that has received much less focus in welfare assessments than stress, but in the long term can be similarly detrimental (Burn 2017; Špinka 2019). If the reported individual differences in the abnormal behaviour–stress link are also present for other abnormal behaviours and in other captive chimpanzee populations, this may help to explain the mixed results found in prior population-level research. For instance, if coprophagy is an expression of stress or boredom for some individuals, while for others it is a neutral product of social learning or a foraging strategy, uniform outcomes are highly unlikely when testing the average of a group comprising a mix of individuals with these particular strategies. Although our analyses in this area remain exploratory and our conclusions therefore tentative, it highlights a key avenue for further theoretical and empirical developments. Interestingly, it has been suggested that learning and copying the crossed-arm walk behaviour by an immigrant female potentially facilitated her social integration (Goldsborough *et al* 2021). In this context, the abnormal behaviour might have had a function for the female unrelated to stress or other indicators of a negative welfare state.

It is important to note that while the presence of stress is often thought to indicate poor welfare, stress is not inherently maladaptive; rather, it is *chronic* elevated stress that is thought to result in a decline in physical and mental well-being (Seery *et al* 2010). Nonetheless, behavioural, pharmacological, and physiological evidence strongly supports the notion that self-scratching behaviour reflects short-term stress (eg Maestripieri *et al* 1992; Schino *et al* 1996; Aureli *et al* 2002), which we consider here as a proxy for a state of poor welfare. However, our results should be interpreted with the additional caution that individual differences may also exist in the tendency to self-scratch (Yamanashi & Matsuzawa 2010). If scratching indicates a short-term increase in stress, so may the exhibition of abnormal behaviours be linked to stress, such as coprophagy in two of the chimpanzees studied here. Therefore, abnormal behaviours could also signal compromised welfare for those individuals in which this link to stressful situations is present.

The notion that individual chimpanzees vary in how they express stress has an interesting parallel and precedent in the human coping literature. Abnormal behaviour can be viewed as an expression of or a response to an unpleasant emotional state — for example, boredom, stress or discomfort — in the past or present. In humans, such unpleasant emotions can manifest behaviourally in a variety of ways. For instance, when experiencing anxiety, some people characteristically bite their nails, while others fidget with their fingers or touch their hair. This diversity of behavioural expressions for a single emotion has been widely studied in humans (Goldstein 1973; Holahan & Moos 1986; DeLongis & Holtzman 2005) and is thought to indicate different underlying coping styles (Goldstein 1973). However, due in part to inherent difficulties associated with measuring or quantifying animal psychological states, individually distinct coping strategies are rarely ascribed to non-human animals. The reported individual variation in abnormal behavioural repertoires, as well as individual variability in the link between coprophagy and stress, both highlight the possibility that chimpanzees, similar to humans, cope with unpleasant situations in different ways and via different behaviours. This additionally raises the interesting possibility that individual abnormal behavioural repertoires may exhibit cross-situational and temporal consistency. In the present study, we pooled the data over time and context (eg indoor/outdoor observations) for pragmatic (sample size) and conceptual reasons (while quantities of abnormal behaviour may vary across context, we had no *a priori* reason to expect that they would differ qualitatively over contexts). Nonetheless, individual abnormal behavioural stability represents an area ripe for further research.

Practically, the conceptual and methodological approach pioneered here can be applied to increase the accuracy and thereby efficacy of behavioural welfare assessments in chimpanzees. Relying on a group-wide, general link between stress and abnormal behaviours could lead to both under- and over-estimations of individual well-being. Individuals with poor welfare might not be recognised as such because they do not show the 'group' pattern of abnormal behaviour; similarly, individuals with good welfare might be mistakenly considered to have poor welfare because their abnormal behaviour is indicative of stress at the group-level, but not for that specific individual. Ideally, a tool would be developed for caretakers and others who work closely with chimpanzees to easily establish which abnormal behaviours could be linked to stressful situations or poor welfare for some individuals, so that they bear this in mind when trying to assess an animal's well-being. A simple observation protocol combined with a comprehensive and thorough list of known abnormal behaviours in chimpanzees aimed to assess the co-occurrence of abnormal behaviours and self-scratching could be a good starting point for such a tool. Importantly, this relies on the validity of the link between self-scratching and stress, and ideally the relationship between abnormal behaviour and stress in an individual would also be examined and validated using additional behavioural and pharmacological methods.

Animal welfare implications

Abnormal behaviours are among the key markers of captive animal welfare. Understanding how such behaviours vary qualitatively across individuals — as opposed to conventional approaches that analyse population-level or quantitative variation in the expression of abnormal behaviour — can yield more refined assessments of animal welfare. Specifically, in chimpanzees, abnormal behavioural repertoires differ systematically across individuals, and may be a unique signature of each chimpanzee's welfare. Combatting the tendency to overgeneralise the function and implications of abnormal behaviours across entire groups or species can help tailor welfare approaches towards the individuals therein.

Conclusion

Though an individual-focused approach to welfare is well-established, the scientific literature tends to foreground more general, group-wide approaches to study the expression of abnormal behaviours. Too often, abnormal behaviour is conceptualised as a uniform category of harmful behaviours indicative of impoverished conditions, overlooking the potential for significant variation between individuals in their expression. The methodological and theoretical approach adopted here, and the new insights to which they lead, caution against this oversight. Individuals have unique behavioural signatures, a reality that the study of abnormal behaviour should also come to reflect.

Declaration of interest

None.

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