Accepted refereed manuscript of: Wallace EK, Herrelko ES, Koski SE, Vick S, Buchanan-Smith HM & Slocombe KE (2019) Exploration of potential triggers for self-directed behaviours and regurgitation and reingestion in zoo-housed chimpanzees. Applied Animal Behaviour Science, 221, Art. No.: 104878. DOI: https://doi.org/10.1016/j.applanim.2019.104878
© 2019, Elsevier. Licensed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International http://creativecommons.org/licenses/by-nc-nd/4.0/

Exploration of potential triggers for self-directed behaviours and regurgitation and reingestion in zoo-housed chimpanzees

Emma K. Wallace [a], Elizabeth S. Herrelko [bcd], Sonja E. Koski [e], Sarah-Jane Vick [b], Hannah M. Buchanan-Smith [b] and Katie E. Slocombe [a]

a)Department of Psychology, University of York, Heslington, York, YO10 5DD

b) Psychology, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA

c) Edinburgh Zoo, Royal Zoological Society of Scotland, Edinburgh EH12 6TS

d) Animal Care Sciences, Smithsonian's National Zoo, 3001 Connecticut Ave NW, Washington DC 20008

e) During Data Collection: Department of Biological Anthropology, University of Cambridge, Pembroke Street, Cambridge, CB2 3QG. Current Affiliation: University of Helsinki, Department of Social Sciences, Unioninkatu 35, 00014

Corresponding Author:

Katie Slocombe

Ks553@york.ac.uk

01904 322905

Exploration of potential triggers for self-directed behaviours and regurgitation and reingestion in zoo-housed chimpanzees

Abstract

The unique challenges faced by animals living in zoos can lead to the production of anxiety-related behaviours. In this study we aimed to understand what specific factors may cause chimpanzees to display these behaviours. In non-human primates, displacement behaviours, such as self-scratching and yawning, are considered markers of anxiety and stress, and Regurgitation and Reingestion (R/R) is considered an abnormal behaviour with negative consequences for physical health. We examined the possible triggers of R/R, scratching, and yawning in a group of zoo-housed chimpanzees and followed this up with an analysis of long-term data to examine further aspects of R/R behaviour. In the first study we conducted focal observations on 18 adult chimpanzees at Edinburgh Zoo, UK, in addition to all occurrence sampling of visitors using flash photography, screaming and banging on the glass in the exhibit. 158 hours of data were analysed and Generalised Linear Mixed Models revealed that yawning was significantly more likely if there was a long period of time since the last feed and when there were moderate numbers of visitors in the zoo. There were trends that yawning was more likely to occur if children screamed and that scratching was more likely to occur if visitors used flash photography. R/R occurred most often within 40 minutes of a feed, but was not affected by the inter-feed interval preceding that feed, positive or negative social interactions, or visitor numbers or behaviour. As there was no obvious daily trigger for R/R, an analysis of long-term data (2009 to 2015) was conducted to investigate if social or dietary factors affected rates R/R over a larger timescale. It was found that R/R rates in the months before a significant diet change were not different from R/R rates in the months after, but it was found that R/R rates decreased over the five-year period. Lastly, we found no evidence that the introduction of individuals engaging in R/R lead to resident chimpanzees habitually adopting the behaviour, despite considerable opportunities to observe it. These findings have implications for welfare interventions aimed to reduce R/R and/or anxiety behaviours in captive populations and for the translocation of individuals that are known to engage in R/R between groups.

Keywords

Regurgitation and Reingestion; Chimpanzees; Animal Welfare; Scratching; Yawning; Anxiety-related behaviour

1. Introduction

Zoo environments present a unique set of challenges, with animals regularly exposed to high numbers of unfamiliar visitors, restricted space, and unnatural social group compositions (Hosey, 2005). Animal welfare is conceived as a balance of positive and negative welfare states, and our goal is to minimise negative and maximise positive welfare (e.g. Mellor and Beusoleil, 2015). It is not only vital for animal welfare, but also valid research findings and the education of visitors, that potential stressors in the zoo environment are identified and, when deemed to be damaging to wellbeing, minimised. For any given species, it is thus important to identify and monitor anxiety-related and abnormal behaviours that may indicate low welfare states and the factors that may trigger their performance.

Within primates, two self-directed behaviours (SDBs), self-scratching and yawning are commonly interpreted as indicators of anxiety (Troisi, 2002; Maestripieri et al. 1992). SDBs are suggested to be coping mechanisms, as wild female olive baboons (*Papio hamadryas anubis*) that display SDBs have lower cortisol levels than those who do not (Higham et al., 2009). The evidence linking self-scratching to anxiety comes from both experimental and observational work: anxiolytic drugs induce scratching in long-tailed macaques (*Macaca fascicularis*;Schino et al., 1991) and natural rates of scratching increase after aggression in Japanese macaques (*Macaca fuscata*; Schino et al., 1998) and when captive chimpanzees (*Pan troglodytes*) perceive the threat of intra-group aggression (Baker and Aureli, 1997). Yawning has also been related to anxiety and viewed as an SDB in primates (Maestripieri et al., 1992), as rates of yawning increase in captive chimpanzees during periods of social tension (Baker and Aureli, 1997) and in wild chimpanzees when in close proximity to humans (Nishida, 1970).

Previous research has indicated that a range of factors can increase anxiety levels in zoo-housed primates, which is manifested in elevated rates of self-scratching and yawning. When not given enrichment, high visitor numbers were associated with high rates of scratching in two groups of captive gorillas (*Gorilla gorilla gorilla*) (Carder and Semple, 2008). In an Indian zoo, where the lion-tailed macaques were often ‘taunted’ by visitors, yawning rates were higher when animals were ‘on-exhibit’ compared to when they were ‘off-exhibit’

(Mallapur et al., 2005).

It is not just high levels of SDBs that can occur in response to captive environments; abnormal behaviours can arise, which are defined as a set of behaviours that are performed either solely in captivity or at a much higher level than in the wild and are thought to be indicators of poor welfare (Birkett and Newton-Fisher, 2011; Mason, 1991; Bloomsmith et al., 2019). A recent study found that 64% of sampled chimpanzees within the United States had been seen to engage in at least one type of abnormal behaviour in the past two years (Jacobson, 2016), which shows that these behaviours are prevalent within captivity. One abnormal behaviour that has been observed across a range of captive primates is regurgitation and reingestion (R/R). It has been observed in chimpanzees (Baker and Easley, 1996), bonobos (*Pan paniscus*) (Miller and Tobey, 2012), gorillas (Akers and Schildkraut, 1985; Hill, 2009), and lion-tailed macaques (Mallapur et al., 2005). The behaviour is defined as the voluntary movement of food from the stomach or the oesophagus into the hand, the mouth or on to a substrate followed by the consumption of the regurgitant (Gould and Bres, 1986). It is similar to rumination, a human abnormal behaviour that can lead to serious health issues, such as oesophageal strictures, ulcers, reflux, oesophagitis, intestinal obstruction, oesophageal motor disorders and pulmonary aspiration (Wyngaarden et al., 1992; Hill, 2009). To date no single trigger for R/R has been identified; rather multiple factors have been suggested. Life history and demographic factors have been shown to influence the likelihood of individuals engaging in R/R. A recent survey of chimpanzees living in research facilities in the United States, conducted by Bloomsmith et al. (2019), found that adults over the age of 40 were more likely to engage in R/R than adults 12- 39 years old, possibly because older adult animals may have lived through a time when the welfare levels within research centres were not as high as today. In addition, non-mother reared/non-wild born individuals living in pairs were more likely to engage in R/R than mother reared or wild born chimpanzees, possibly due to the lack of mother rearing. It has been shown that being deprived of mother rearing can cause emotional trauma and lead to the development of abnormal behaviours (Kalcher et al., 2008).

Indeed, rumination in humans has been linked to anxiety (Landis and Lambroza, 2001), which suggests that this could also be a more immediate trigger for the behaviour in animals. Previous research has suggested other immediate triggers for R/R may include boredom (Baker, 1997, 2004), diet (Morgan et al., 1993; Lukas

et al., 2014) and visitor presence and behaviour (Mallapur et al., 2005; Wells, 2005). Taken together, it seems a range of factors may influence engagement in this behaviour, with some suggesting a link to current or previous stress, but a lack of consistency across studies and populations highlights a need for further research. A better understanding of the causes of R/R may enable effective interventions to be implemented, which would be valuable as R/R is likely to be negatively perceived by zoo visitors (Ackers and Schildkraut, 1985) and could affect the educational potential of the exhibit by giving false impressions of the species (Carlstead, 1998; Ironmonger et al., 1992; Ackers and Schildkraut, 1985).

In order to reduce anxiety-related and abnormal behaviours in zoo-living animals, it is first important to understand the aspects of this captive environment that may increase stress or abnormal behaviour. Zoo visitors are a potential source of anxiety, in terms of their numbers and behaviour. For example, mandrills (*Mandrillus sphinx)* exhibit higher levels of leg/hair pulling, stereotyped locomotion and masturbation in the presence of high visitor numbers (Chamove et al., 1988). In terms of visitor behaviour, in a multi-species study at Sacramento zoo it was found that active groups of visitors (where at least one individual attempted to attract an animal's attention), regardless of size, induced more locomotion and audience-directed behaviours than passive groups, although the authors do not state if they believed that was a sign of a positive or negative welfare change (Mitchell et al., 1992). Previous studies have found, however, that the activity or noise level of visitors negatively affects the behaviour of captive primates (Chamove et al., 1988; Birke, 2002). If the presence or behaviour of visitors in zoos has a negative effect on animal welfare then more research is needed into exactly which behaviours and numbers of visitors causes these effects and how they can be minimised.

The type and availability of food in captive environments are very different from that found in most species' natural environments (Oftedal and Allen, 1996) and, therefore, feeding regimes could be a potential source of stress and/or triggers for R/R. Fruit and starchy vegetables increased R/R rates in laboratory chimpanzees and zoo-housed gorillas (Morgan et al., 1993; Lukas et al., 2014). In addition, increasing the amount of time since eating has also been linked to higher R/R rates in chimpanzees (Baker and Easley, 1996). This may be due to longer periods between feeds violating anticipated feeding times, as delays to expected feeds increases abnormal behaviours in macaques (Waitt & Buchanan-Smith, 2001).

Agonistic interactions with conspecifics can be a source of anxiety, leading to higher rates of SBDs (Castles et al., 1999), but affiliative interactions can be a protective factor against abnormal behaviours and anxiety-related behaviours. For instance, in captive bonobos, R/R was positively correlated with aggression, but negatively correlated with social grooming (Miller and Tobey, 2012). It is unclear whether these social behaviours had a direct casual impact on R/R behaviour or whether the relationship was mediated through changes in stress levels, however it highlights the importance of considering social factors in the occurrence or rate of abnormal behaviour such as R/R.

Given the importance of minimising factors that cause anxiety or facilitate the development of abnormal behaviours in captive animals, we investigated the possible triggers of SDBs and R/R in a large group of zoo-housed chimpanzees at Edinburgh Zoo over two studies. We chose to investigate R/R within this group as it was regularly observed in a number of individuals, whereas other abnormal behaviours were too infrequent or displayed by too few individuals to generate sufficient data in the time-period available. In the first study, to test whether environmental factors affected the production of the behaviours, we examined whether the length of time between feeds, the type of food the animals received, grooming within the group, visitor behaviour, and the number of visitors in the zoo effected the occurrence of self-scratching, yawning, or engaging in R/R. In the second, we investigated longer-term influences on R/R prevalence in the group. In study 1, we predicted that high visitor numbers would cause an increase in rates of R/R and SDBs, in line with previous findings (Carder and Semple, 2008; Mallapur et al., 2005). Previous work has shown that the behaviour of zoo visitors can have negative effects on the behaviour of zoo animals (Hosey, 2000). We predicted that zoo visitors displaying specific potentially negative behaviours that have previously been observed at this facility (screaming, banging on windows, flash photography) would increase rates of SDBs and R/R. In terms of social interactions with group members, we predicted that being involved in social grooming would decrease an individual's rates of R/R and SDBs (Miller and Tobey, 2012). We predicted that that SDB and R/R rates would increase when the duration between feeds was long (Baker and Easley, 1996) and finally that consumption of fruit and starchy vegetables would increase rates of R/R (Morgan et al., 1993; Lukas et al., 2014).

2. Study One: Investigation into potential triggers of scratching, yawning and R/R

2.1 Methods

2.1.1 Study Site

The study was undertaken at Budongo Trail Chimpanzee enclosure, Edinburgh Zoo, Scotland. The enclosure comprises of three large indoor areas or 'pods' that include wooden climbing structures, a bedding area, smaller 'pods' used for conducting cognitive research and an outdoor enclosure with further climbing structures. These areas are all connected by tunnels and the whole enclosure spans over 1500m^2 (see Herrelko et al., 2015 for more details) This layout allows the animals to split into sub-groups that vary in composition of individuals, allowing their natural fission-fusion social system to be expressed. Budongo Trail exhibit receives approximately 800,000 visitors each year (Whitehouse et al., 2014).

2.1.2 Subjects

The group of chimpanzees at Edinburgh Zoo comprised of two recently integrated groups (Schel et al., 2013) that originated from Edinburgh (EZ) and Beekse-Bergen Safari Park (BB), The Netherlands (see Table S1 for individual demographic details). The BB chimpanzees were introduced in 2010 and prior to living at the Beekse-Bergen Safari Park in 2007, these individuals were housed in a medical testing facility and their history was largely unknown.

2.1.3 Data collection

Data collection occurred over two study periods; 13th March 2014 to 8th July 2014 and 6th January 2015 to 2nd March 2015. Ethical approval was obtained from the Animal Welfare Ethical Review Board of the Dept. of Biology, University of York. Twenty minute focal samples (Altmann, 1974) were carried out on all 18 adult individuals within the group (mean = 27.8 samples/individual; range = 20-57). No more than three consecutive focal samples, lasting an hour in total, were collected within each 'pod' within the enclosure. No animal was observed more than once each day and individuals with the least focal minutes were preferentially chosen as focal animals from those available in the pod. Only complete focal samples where the individual was observed for the full 20 minutes were included in the analysis, making a total of 474 focal samples (158 hours). During the focal period, we used one/zero sampling to record if visitors used flash photography (Y/N), percussed (banging, tapping etc.) on the windows of the enclosure (Y/N) and if children screamed or vocalised loudly (Y/N). All occurrence data were collected on whether the focal individual was

involved in dyadic grooming (including roles in these interactions; self-grooming was not recorded) whilst the frequency of yawning, scratching and engaging in R/R were recorded. To be counted as separate events, an inter-event period of at least 2 seconds was required for all behaviours (e.g. two yawns 1 second apart would be counted as 1 yawn; two scratches 5 seconds apart would be counted as 2 events). Due to the large number of samples where zero events were recorded, the frequency data we collected was extremely skewed and transformation was ineffective. Therefore, we converted these behavioural measures into categorical variables where the behaviour was either present or absent within a focal sample period.

Examination of the visitor number data through Q-Q plots and the acquisition of significant Shapiro-Wilk tests of normality indicated that this variable was also not normally distributed, even after transformation. Therefore, this variable was also converted into a categorical variable. Total visitor numbers within the zoo (data based on gate numbers provided by Edinburgh Zoo) were categorised into low (0-1000), medium (1001-4000) and high (4000+) visitor numbers. The category boundaries for this variable was chosen as they gave a roughly equal distribution of data in each category.

The keepers provided detailed records of the time, type and quantities of food given to the chimpanzees on a daily basis. Food data were categorised based on methods used by Plowman (2013) into starchy vegetables, fruit or other. If feeds were given that contained multiple food types, each type of food was categorised separately so there were multiple data points for that feed. To account for taking multiple samples from some feeding events, feeding event was entered as a random factor into our statistical models. Before data analysis was undertaken, it was noted that only six of the 18 chimpanzees were regularly seen to engage in R/R and the majority of these events (16 out of a total of 27 observed during study period; 59.3%) happened within 40 minutes of the most recent feed. For these reasons, the data for all analysis of R/R came from just those six chimpanzees and focal samples that occurred within 40 minutes of a keeper feeding event.

2.2 Data Analysis

2.2.1 Statistical Analysis

General Linear Mixed Models (GLMMs) with a binomial error structure and a logit link were used to investigate the influence of categorical and continuous explanatory variables on whether or not the chimpanzees displayed the behaviours in question. Individual identity was included as a random factor to

address the issue of pseudoreplication due to each individual contributing multiple data points to the analyses. Likelihood ratio tests were run for full models and to determine the contribution of each variable in the model. If a factor that explained significant variation in a dependent variable contained three categories, post-hoc GLMMs were run, each containing two of the three categories within the factor. All tests were run using SPSS v.21 with an alpha value of .05, but with Bonferroni corrected alpha levels of .017 applied to post hoc tests.

Table 1 shows each of the research questions and the breakdown of the variables included in each of the GLMMs that were run in order to answer each of those questions. For question (iv) that related to R/R, as the majority of R/R events were observed occurring when food was available during or shortly before the focal observation period, we looked at if the duration between the most recent feed (within the last 40 minutes from the focal period) and the previous feed affected the occurrence of R/R. The sample was limited to sessions where the previous feeding opportunity was known (i.e. sessions where the previous feed was the day before were omitted to control for opportunistic overnight eating).

------Table 1 ----

2.3 Results

2.3.1 Descriptive Results

The raw frequencies of scratching, yawning and R/R events can be seen in Table S2. The proportion of focal samples (N = 474) where the focal individual was observed (i) scratching was 0.62, (ii) yawning was 0.20 and (iii) engaging in R/R was 0.04. For R/R, if we just examined data from the six individuals who had been known to regularly engage in R/R prior to the study period, they were observed to engage in R/R in 0.15 of their total 183 focal samples or 0.28 of the 68 focal samples within 40 minutes of a feed. Although the likelihood of yawning and scratching occurring was higher in the six individuals who regularly engaged in R/R compared to the 12 individuals who did not regularly engage in R/R, this pattern was not significant (Median proportion of focal samples where yawning occurred for R/R individuals = 0.23 (IQR = 0.20) and for Non R/R individuals = 0.16 (IQR = 0.06); Mann Whitney U test U = 24.50, p = .279; Median proportion of focal samples where scratching occurred for R/R individuals = 0.63 (IQR = 0.12) and for Non R/R individuals = 0.56 (IQR = 0.30); Mann Whitney U test U = 27.50, p = .425)

235

236 *2.3.2 Does the number of visitors affect SDBs and R/R in chimpanzees?*

237 Visitor numbers in the zoo did not explain a significant amount of variation in whether R/R or scratching
238 behaviour occurred (Table 2) but did explain a significant amount of variation in whether the chimpanzees
239 yawned (Table 2). Post-hoc GLMMs revealed that a significantly higher proportion of focal samples contained
240 yawning when there were a medium number of visitors in the zoo compared with a low number of visitors
241 ($F = 8.13$ (1, 402), $p = 0.005$; Figure 1). The likelihood of the focal chimpanzee yawning was not different for
242 any other pairwise comparisons in the post-hoc GLMMs (see table S3).

243 ------Table 2 -----

244 ------Figure 1 -----

245 *2.3.3 Does visitor behaviour affect SDBs and R/R in chimpanzees?*

246 None of the different types of potentially disruptive visitor behaviours explained a significant amount of
247 variation in whether or not the chimpanzees engaged in R/R (Table 2). Overall visitor behaviour did not
248 explain a significant amount of variation in whether or not chimpanzees scratched (Table 2), however, when
249 individual factors within the model were examined, there was a trend for a higher proportion of focal samples
250 to contain scratching when flash photography was used (0.70) than when it was absent (0.59; Table 2). Again,
251 overall visitor behaviour did not explain a significant amount of variation in whether or not chimpanzees
252 yawned but there was a trend for a higher proportion of focal samples to contain yawning when children
253 screamed (0.26) than when they did not (0.18; Table 2).

254 *2.3.4 Does involvement in grooming affect SDBs and R/R in chimpanzees?*

255 Receiving or giving grooming at any time during the focal period did not affect whether or not the
256 chimpanzees engaged in R/R, scratched or yawned (Table 2).

257 *2.3.5 Does length of time since being fed affect SDBs and R/R in chimpanzees?*

258 The amount of time from the most recent feeding event influenced the likelihood of yawning, which
259 increased as interval between feeding increased (Figure 2), but not the likelihood of scratching or R/R (Table
260 2).

261 ----Figure 2-----

2.3.6 Does the type of food consumed affect the likelihood of Regurgitation and Reingestion?

The type of food given did not affect R/R ($F(2,88) = 1.05$ $p=0.354$).

2.4 Discussion

The main finding of this study is that, contrary to the predictions, few of the potential environmental triggers we examined significantly affected the occurrence of SDBs or R/R within this group of chimpanzees. One factor of the captive environment we did find to contribute to increases in SDBs was the duration between feeding events. In the wild, chimpanzees spend 6.68 hours per day foraging or eating (Leonard and Robertson, 1994) whilst in captivity this is greatly reduced (Chamove et al., 1982) and can mean that there are long periods of time between feeding events. Our results show that when the chimpanzees have to wait longer to eat they are more likely to yawn. Apart from one visitor talk feed which occurs at a standard time each day, the keepers aimed to feed at irregular intervals to prevent anticipatory behaviours, and it is unlikely that yawning is an anticipatory response in this group. Automatic feeders that release food at specific times or random intervals could help negate this issue and reduce potential stress in captive chimpanzees.

Several studies have shown that high visitor numbers can negatively affect behaviour (Birke, 2002) leading us to predict that having a high number of visitors would lead to an increase in SDBs. We found no evidence of visitor numbers affecting scratching or R/R, but, in line with our prediction, we did find that there was a higher proportion of focal samples where the focal animal yawned when there were medium zoo gate numbers (1001 to 4000 people) compared to low number of visitors (0-1000). However, contrary to the prediction, yawning was not more likely when high rather than medium or low numbers of visitors were in the zoo. This result is unexpected and shows that further research into other associated factors, such as duration of visitor stay at enclosure windows and visitor noise levels, are required to establish what is driving this effect. Although visitor behaviour did not explain a significant amount of variation in whether SDBs or R/R occurred, there were trends for yawning being more likely when children were screaming and scratching being more likely when flash photography was used. This highlights these visitor behaviours as potentially problematic, and future research with more groups and individuals is needed to investigate these factors further.

Another unexpected result was that grooming did not appear to influence the likelihood of SDBs or R/R. This

contrasts with work on long-tailed macaques (Schino et al., 1988), crested black macaques (Aureli and Yates, 2010), and bonobos (Miller and Tobey, 2012), but supports previous findings in barbary macaques (*Macaca sylvanus*) (Semple et al., 2013). Semple et al. suggest that when the macaques terminated a grooming event it may have led to an increase in anxiety, which counter-acted the positive, anxiety reducing effect of grooming that would have been expected to lead to a reduction in scratching.

Previous research has suggested that the type of food given to the chimpanzees (Morgan, 1993) and increased time between feeds (Baker and Easley, 1996) can affect R/R behaviour, however, this was not found to be the case with this group of animals. Although we found no evidence that R/R was linked to potentially stressful concurrent events, we had an excellent opportunity to track whether large scale events affected the frequency of this behaviour.

3. Study Two: Longer-term influences on R/R prevalence

3.1 Aims and Research Questions

Given the lack of immediate factors influencing R/R in this group, we wanted to investigate longer term influences on this behaviour. More specifically we aimed to examine if the translocation and integration into a new social group and major diet changes affected the rates of R/R. We also examined the stability of R/R rates from 2009 to 2015. Analyses were focussed on the nine of the 11 BB chimpanzees who were integrated into the Edinburgh group in 2010, were still alive in 2015 and who had relatively high levels of R/R behaviour at their previous facility. These nine individuals included all six individuals who were observed to engage in R/R in study one. In addition, given that anecdotal reports from keepers and researchers indicated that the original EZindividuals did not engage in R/R prior to the arrival of the BB group, we wanted to test whether this behaviour spread through social learning. Many chimpanzees in captivity are moved between facilities for breeding programmes so it is important to understand if this is a socially learnt negative behaviour, as coprophagy has been suggested to be (Hopper et al., 2016).

More specifically, in our second study we aimed to address the following questions:

1) Did the introduction of the BB individuals to Edinburgh Zoo cause their R/R rates to increase? It was predicted that R/R rates would increase during the introduction between the two groups of individuals as this was believed to be a stressful time for the animals.

2) Are any changes in R/R rates related to changes in the diet given to the chimpanzees? Changes in the chimpanzees' diet, as recommended by zoo veterinarians and nutritionists in order to improve the digestion of the BB individuals, may have led to changes in R/R rates. Mulder et al. (2016) found that changes to the diet of the chimpanzees at Amersfoort Zoo by increasing fibre did lead to a significant reduction in R/R rates but descriptive data showed that the rates of R/R were lowest immediately after the change in diet and began to increase afterwards.

3) Did R/R rates in BB individuals change over time? Being integrated into a large and socially complex group living in an enclosure designed to encourage natural behaviours, such as 'fission-fusion' dynamics (Aureli et al., 2008), in addition to several small diet changes over this period could have led to reductions in the BB individuals' rates of R/R.

4) Did observing R/R in the BB individuals lead to the adoption of the behaviour by EZ individuals? We predicted that R/R might be socially learnt, which would mean that observing the BB individuals engaging in R/R could lead to the performance and adoption of the behaviour by the EZ individuals.

3.2 Methods

The data analysed in this study was collected during three distinct time periods, which are described in detail below. Each data collection used slightly different methodologies but they were similar enough to allow this very important long-term analysis to be undertaken.

1) May to September 2009 at Beekse-Bergen Safari Park. Data were collected by SK and students using 10-minute long focal samples (Altmann, 1974) to record the duration of time spent engaging in R/R by the focal individual. Prior to data collection, inter-observer reliability test between SK and each student showed >90% identical data coding. 836 focal samples were collected (139.3 hours). 836 focal samples were collected (139.3 hours).

2) March to October 2010 at Edinburgh Zoo (pre-, during and immediately post integration of BB and EZ groups) 10-minute focal samples were conducted and the frequency of R/R within each sample period recorded. Data were collected by ESH and 2 research assistants, with interobserver reliability tested at 2 time points and agreement on presence or absence of R/R completely reliable (R = 1.0). 1133 focal samples were collected (188.8 hours).

3) July 2010 to February 2015 at Edinburgh Zoo. Much of the data from this time period came from University of York researchers working on independent research projects in 2010-11, as well as long-term observational data collection that was introduced in 2012 by KS. All long-term researchers conducting independent research projects at Budongo Trail contributed to the data set, once they had passed an identification test to ensure they could reliably identify all individuals. Detailed instructions were given to researchers and they submitted data regularly for checking by KS or EW, so they received feedback on their data collection, but no formal measures of interobserver reliability were taken. 10-minute focal samples were conducted where all instances of the focal engaging in R/R were recorded, along with details of which other chimpanzees were in the same pod as the focal animal and which of those were within 3 meters of the focal individual at the time of each R/R event. Data on changes to diets and the dates of the integration process were obtained from the keepers. 3612 focal samples were collected (602 hours).

In order to make all three sets of data comparable, each focal observation was scored for whether or not at least one R/R event occurred in the 10-minute time period and only complete focal periods were considered.

3.3 Data Analysis

3.3.1 Are the changes to R/R related to the integration process?

Individual proportions of focal observations where R/R was observed per month for the BB individuals were calculated. These monthly proportions were averaged for three time periods: pre-integration of the BB individuals (May to September 2009), during the integration (May to July 2010) and immediately post integration (August to December 2010). A Friedman test (N= 9) was used to compare the average rates of R/R for the three time periods.

3.3.2 Are the changes to R/R related to diet changes?

The monthly proportion of focal observations where R/R was observed for the BB individuals, were used to compare the average R/R rates of the three months before and after a major diet change. On 20th October 2010 an additional 50kg of grapes, pears and mangos, 15kg of apples and four loaves of white bread were included in the weekly diet of the chimpanzees. Individuals were observed for a minimum of 18 focal samples (three hours) during each three- month period. A Wilcoxon test (N= 9) was used to compare the mean of the proportions of observations where R/R occurred in each three-month period before and after the diet

change.

3.3.3 Have the proportion of focals where R/R was observed changed over time?

For each year, from 2009 to 2015, a yearly proportion of focals where R/R was observed for each individual was calculated by averaging the available monthly proportions in each year. These values for the 9 BB individuals were then averaged to create a group annual mean. The relationship between time (year) and R/R proportions was examined using a Kendall's-tau correlation, due to the small sample size.

3.3.4 Have the EZ individuals socially learnt the behaviour from the BB individuals?

We wanted to establish if observing the BB chimpanzees engaging in R/R lead to the EZ individuals adopting the behaviour. We calculated the total number of R/R events that the BB individuals were recorded as engaging in. We also determined the number of these events where at least one EZ chimpanzee was present within 3 metres of a BB individual, from where they could have observed the behaviour closely. The data used for this came from August 2010 – 2015, once the BB had been fully integrated into the group. We then calculated the total number of times each of the EZ individuals were recorded to have engaged in R/R to see if the behaviour was adopted by those animals.

3.3.5 Statistical analysis

All tests run were two-tailed with alpha level set at 0.05 and Bonferroni corrected to p= 0.017 for post hoc tests. Wilcoxon Signed Ranks, Friedmans and Kendall's-tau tests were run using SPSS v.21. Effect sizes (*d and r*) were calculated using an online tool (http://www.uccs.edu/~lbecker/). When using Cohen's *d* as an effect size, .80 is considered a large effect, .50 a medium sized effect, and 0.20 a small effect (Cohen, 1992). *r* was used as an effect size for non-parametric Wilcoxon Signed Rank tests, in which 0.50 or above is a large effect, above 0.30 a medium effect and 0.10 a small effect (Pallant, 2007).

3.4 Results

3.4.1 Are the changes in R/R related to the integration process?

There were significant differences between the proportions of observations where R/R occurred pre-, during and post integration (Friedman $X^2(2) = 9.60$ N= 9, p=0.008; Figure 3). Using Bonferroni corrected alpha levels, post-hoc Wilcoxon signed ranks tests show that the proportions of R/R were significantly higher in the pre-integration than during the post-integration period (Z= -2.38, p=0.017; *r*= 0.24). There were trends for the

proportions of R/R being higher during pre-integration than in the integration period (Z= -2.24, p=0.025; r=0.61) and in integration than post-integration (Z= -2.20, p=0.028; r=0.50). Figure 3 illustrates that all individuals observed to engage in R/R showed a decrease over the integration process and that this pattern was not driven by a single individual.

----Figure 3 -----

3.4.2 Are the changes in R/R related to diet changes?

R/R proportions were not significantly higher after the diet change (median = 0.073; IQR = 0.13) than before (median = 0.071; IQR = 0.16; Wilcoxon Z= -0.41 N= 10 p=0.686; *r*= 0.16).

3.4.3 Has the proportion of focals where R/R was observed changed over time?

There was a trend for the proportion of focals where R/R was observed decreasing over the period from 2009 to 2015 (τ_b = -0.62, *n* = 9, *p*= 0.051). Figure S4 shows how proportions of R/R change over time for nine BB individuals and indicates that all individuals contribute to the overall group decrease rather than one individual driving it.

3.4.4 Have the EZ individuals socially learnt the behaviour from the BB individuals?

We found that the EZ chimpanzees were within 3 metres of 89 R/R events and the BB chimpanzees were recorded to engage in R/R a total of 160 times from August 2010-2015, which means that the EZ chimpanzees were in proximity to 55.6% of all observed R/R events. Despite this, no EZ individual was seen to engage in R/R themselves more than four times between August 2010 and July 2013 (see Table S5). The number of R/R events by the EZ individuals was low and sporadic and no events were recorded after July 2013.

3.5 Discussion

It was predicted that observations of R/R would increase during the introduction between the two groups of individuals as this was believed to be a stressful time for the animals. However, R/R proportions were significantly higher before the introduction. This suggests that either the integration process did not involve as much negative stress as assumed or more likely, given the convergent results of study 1, R/R is not a response to current stress levels. It is possible that R/R is related to boredom (Baker, 1997; 2004) and that the cognitive challenge presented to the BB chimpanzees by the introduction to a new physical and social environment may have reduced their boredom and, therefore, their proportions of focal samples where R/R

was observed. Previous studies have found that the provision of foraging related enrichment (Baker, 1997) and increased human caretaker interaction (Baker, 2004) has led to reductions in R/R rates. We therefore recommended that further research investigating the link between boredom and R/R should be undertaken. In October 2010, the diet of the chimpanzees changed and the amount of fruit given weekly increased. Based on the results of Morgan et al. (1993) it was predicted that this would lead to an increase in R/R. However, comparing the proportions of R/R for three months on either side of this diet change showed there was no significant difference, however, this could have been because rates were already low before the change (only 8/743 samples prior to the diet change contained an R/R event). There were other small changes to the diet of these chimpanzees from April 2010 onwards but we lacked sufficient data to examine three months prior to and after each of these changes. It is possible, therefore, that each of these small changes may have contributed to the overall reduction in R/R within the BB individuals.

By looking longitudinally at the R/R performed by the chimpanzees at Edinburgh Zoo we have been able to identify that the proportion of the BB individuals' focal periods where R/R was observed has a trend for reducing over time, which suggests an improvement in their welfare. Some BB individuals (Pearl, Edith, Eva and Heleen) were no longer observed engaging in R/R by 2015. The design of Budongo Trail and being part of the large, socially complex group of chimpanzees is the most probable cause of the reduction of R/R rates since 2009 in the BB individuals. The fact that six of the animals still occasionally engage in R/R is likely due to the persistent nature of the behaviour and is possibly a form of coping strategy, similar to stereotypical behaviours (Higham et al., 2009). In humans, the same behaviour, known as rumination (Nakanishi and Anderson, 1982), has been linked to periods of distress in individuals of average intelligence but the behaviour is very difficult to eradicate (Nakanishi and Anderson, 1982). Mulder et al. (2016) found that feeding a higher fibre diet did reduce rates of R/R in the chimpanzees at Amersfoort Zoo but the behaviour did not disappear, suggesting the behaviour had become a habit. Although we do not know the full history of the BB animals during their time in the medical testing facility, it is likely that the experience may have been stressful and this is where they first performed R/R. Once established as a behaviour pattern, it may be difficult to eliminate, hence why the BB individuals still perform the behaviour, albeit at much lower levels.

It was predicted that R/R might be socially learnt but whilst nine of the 11 EZ individuals were recorded as

451 engaging in R/R, only 18 instances were observed from integration with the BB group (July 2010) to July
452 2013. The first recorded instances of R/R by EZ individuals were during October 2010 and R/R then occurred
453 rarely until 2013, after which time the behaviour seemingly disappeared. Prior to July 2010 and the start of
454 the integration, R/R was not systematically monitored for the EZ group because it was very rarely observed
455 by keepers and therefore was not considered a welfare issue. Despite having ample opportunity to observe
456 the behaviour being displayed by the BB chimpanzees, the behaviour was only ever performed at negligible
457 rates by the EZ individuals. This study demonstrates that the integration of individuals that engage in R/R
458 into an established group that does not regularly display the behaviour does not seem to lead to the spread
459 of the behaviour.

460 **4. Conclusions**

461 Our two studies together show that surprisingly few environmental events were associated with increases in
462 SBDs or R/R in this group of zoo-housed chimpanzees. Yawning was significantly more likely to occur when
463 the period between feeds was greater and when there were a medium rather than low number of visitors in
464 the zoo, but visitor behaviour and grooming within the group did not significantly influence SBDs. We also
465 found no links between R/R and environmental stressors as neither the presence nor behaviour of visitors
466 affected the production of the behaviour and the number of observed R/R events actually decreased during
467 and after the social integration of the two groups. No obvious trigger for R/R was identified for this group,
468 suggesting it may be a behaviour that has persisted from previous periods of potentially suboptimal
469 conditions. However, R/R decreased in frequency following integration into a complex physical and social
470 environment. We also demonstrated that the movement of individuals known to engage in this behaviour
471 into groups where R/R is absent is unlikely to lead to the spread of this behaviour.

472 **Acknowledgements**

473 We are grateful to RZSS and the keepers of Budongo Trail for their permission and support in conducting this
474 research. Thanks to Jeffrey Ridder, Annette van de Kraats, Thomas Bionda, Lauren Marshall, Joana Griciute
475 and long-term researchers at Budongo Trail who assisted with data collection. Funding for ESH was provided
476 by University of Stirling, Burning Gold Productions (with the BBC and Animal Planet), the Royal Zoological
477 Society of Scotland, and the Scottish Funding Council.

478 **References**

479 Akers, J. S., & Schildkraut, D. S. (1985). Regurgitation/reingestion and coprophagy in captive gorillas. *Zoo*
480 *Biology*, *4*(2), 99-109.

481 Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227-266.

482 Aureli, Filippo, Colleen M. Schaffner, Christophe Boesch, Simon K. Bearder, Josep Call, Colin A. Chapman,
483 Richard Connor et al. (2008) "Fission-fusion dynamics: new research frameworks." *Current Anthropology*,
484 *49(4),* 627-654.

485 Aureli, F., & Yates, K. (2010). Distress prevention by grooming others in crested black macaques. *Biology*
486 *letters*, *6*(1), 27-29.

487 Baker, K. C. (1997). Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. *Zoo*
488 *Biology*, *16*(3), 225-236.

489 Baker, K. C. (2004). Benefits of positive human interaction for socially-housed chimpanzees. *Animal Welfare*,
490 *13*(2), 239.

491 Baker, K. C., & Aureli, F. (1997). Behavioural indicators of anxiety: an empirical test in chimpanzees.
492 *Behaviour*, *134*(13), 1031-1050.

493 Baker, K. C., & Easley, S. P. (1996). An analysis of regurgitation and reingestion in captive chimpanzees.
494 *Applied Animal Behaviour Science*, *49*(4), 403-415.

495 Birke, L. (2002). Effects of browse, human visitors and noise on the behaviour of captive orangutans. *Animal*
496 *Welfare, 11*(2), 189-202.

497 Birkett, L. P., & Newton-Fisher, N. E. (2011). How abnormal is the behaviour of captive, zoo-living
498 chimpanzees?. *PloS one*, *6*(6), e20101.

499 Bloomsmith, M. A., Clay, A. W., Lambeth, S. P., Lutz, C. K., Breaux, S. D., Lammey, M. L., ... & Mareno, M. C.
500 (2019). Survey of Behavioral Indices of Welfare in Research Chimpanzees (Pan troglodytes) in the United
501 States. *Journal of the American Association for Laboratory Animal Science*, *58*(2), 160-177.

502 Carder, G., & Semple, S. (2008). Visitor effects on anxiety in two captive groups of western lowland gorillas.
503 *Applied Animal Behaviour Science*, *115*(3), 211-220.

504 Carlstead, K. (1998). Determining the causes of stereotypic behaviors in zoo carnivores: toward appropriate

505 enrichment strategies. *Second nature: Environmental enrichment for captive animals*, 172-183.
506 Castles, D. L., Whiten, A., & Aureli, F. (1999). Social anxiety, relationships and self-directed behaviour among
507 wild female olive baboons. *Animal Behaviour*, *58*(6), 1207-1215.
508 Chamove, A. S., Hosey, G. R., & Schaetzel, P. (1988). Visitors excite primates in zoos. *Zoo Biology*, *7*(4), 359-
509 369.
510 Chamove, A. S., Anderson, J. R., Morgan-Jones, S. C., & Jones, S. P. (1982). Deep woodchip litter: hygiene,
511 feeding, and behavioral enhancement in eight primate species.
512 Cohen, J. (1992). A power primer. *Psychological Bulletin*, *112*(1), 155.
513 Gould, E., & Bres, M. (1986). Regurgitation and reingestion in captive gorillas: description and intervention.
514 *Zoo Biology*, *5*(3), 241-250.
515 Herrelko, E.S., Buchanan-Smith, H.M., & Vick, S-J. (2015). Perception of Available Space During Chimpanzee
516 Introductions: Number of Accessible Areas Is More Important Than Enclosure Size. *Zoo Biology*, 34, 397-405.
517 Higham, J. P., MacLarnon, A. M., Heistermann, M., Ross, C., & Semple, S. (2009). Rates of self-directed
518 behaviour and faecal glucocorticoid levels are not correlated in female wild olive baboons (*Papio hamadryas*
519 *anubis*). *Stress*, *12*(6), 526-532.
520 Hill, S. P. (2009). Do gorillas regurgitate potentially-injurious stomach acid during 'regurgitation and
521 reingestion?'. *Animal Welfare*, *18*, 123-127.
522 Hopper, L. M., Freeman, H. D., & Ross, S. R. (2016). Reconsidering coprophagy as an indicator of negative
523 welfare for captive chimpanzees. *Applied Animal Behaviour Science*, *176*, 112-119.
524 Hosey, G. R. (2000). Zoo animals and their human audiences: what is the visitor effect? *Animal Welfare*, *9*(4),
525 343-358.
526 Hosey, G. R. (2005). How does the zoo environment affect the behaviour of captive primates?. *Applied Animal*
527 *Behaviour Science*, *90*(2), 107-129.
528 Ironmonger, J., Ironmonger, S., & Heaton, R. (1992). *The Good Zoo Guide*. HarperCollins.
529 Jacobson, S. L., Ross, S. R., & Bloomsmith, M. A. (2016). Characterizing abnormal behavior in a large
530 population of zoo-housed chimpanzees: prevalence and potential influencing factors. *PeerJ*, *4*, e2225.

Kalcher, E., Franz, C., Crailsheim, K., & Preuschoft, S. (2008). Differential onset of infantile deprivation produces distinctive long-term effects in adult ex-laboratory chimpanzees (Pan troglodytes). *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology*, *50*(8), 777-788.

Landis, B., & Lambroza, A. (2001, March). A respiratory biofeedback solution for the rumination syndrome. In *Biological Psychology* (Vol. 56, No. 1, pp. 79-80)., NETHERLANDS: ELSEVIER SCIENCE BV.

Leonard, W. R., & Robertson, M. L. (1994). Evolutionary perspectives on human nutrition: the influence of brain and body size on diet and metabolism. *American Journal of Human Biology*, *6*(1), 77-88.

Lukas, K. E., Bergl, R., Ball, R., Kuhar, C. W., Lavin, S. R., Raghanti, M. A., ... & Dennis, P. M. (2014). Implementing a low-starch biscuit-free diet in zoo gorillas: The impact on health. *Zoo Biology*, *33*(1), 74-80.

Maestripieri, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour*, *44*(5), 967-979.

Mallapur, A., Sinha, A., & Waran, N. (2005). Influence of visitor presence on the behaviour of captive lion-tailed macaques (*Macaca silenus*) housed in Indian zoos. *Applied Animal Behaviour Science*, *94*(3), 341-352.

Mellor, D. J., & Beausoleil, N. J. (2015). Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare*, *24*(3), 241-253.

Mason, G. J. (1991). Stereotypies: a critical review. *Animal Behaviour*, *41*(6), 1015-1037.

Miller, L. J., & Tobey, J. R. (2012). Regurgitation and reingestion in bonobos (*Pan paniscus*): Relationships between abnormal and social behavior. *Applied Animal Behaviour Science*, *141*(1), 65-70.

Mitchell, G., Tromborg, C. T., Kaufman, J., Bargabus, S., Simoni, R., & Geissler, V. (1992). More on the 'influence' of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science*, *35*(2), 189-198.

Morgan, L., Howell, S. M., & Fritz, J. (1993). Regurgitation and reingestion in a captive chimpanzee (*Pan troglodytes*). *Lab Animal*, 22:42-45.

Mulder, I., van der Meer, R., de Vries, H., & Sterck, E. H. M. (2016). The relationship between diet change and regurgitation and reingestion in captive chimpanzees. *Journal of Zoo and Aquarium Research*, *4*(4), 196.

Nakanishi, D. A., & Anderson, D. R. (1982). Behavioral Treatment of Psychogenic Vomiting Among Children-A Review and Case Example. *Journal Of Psychosocial Nursing And Mental Health Services*, *20*(11), 17-20.

558 Nishida, T. (1970). Social behavior and relationship among wild chimpanzees of the Mahali Mountains.
559 *Primates*, *11*(1), 47-87.
560 Oftedal, O. T., & Allen, M. E. (1996). Nutrition and dietary evaluation in zoos. In Wild mammals in Captivity.
561 109–116. Kleiman, D. G., Allen, M. E., Thompson, K. V., & Lumpkin, S. (Eds). Chicago, IL: The University of
562 Chicago Press.
563 Pallant, J. (2007). *SPSS Survival Manual.* 3rd edition. McGrath Hill.
564 Plowman, A. (2013). Diet review and change for monkeys at Paignton Zoo Environmental Park. *Journal of*
565 *Zoo and Aquarium Research*, *1*(2), 73-77.
566 Schel, A., Rawlings, B., Claidiere, N., Wilke, C., Wathan, J., Richardson, J., ... & Slocombe, K. (2013). Network
567 analysis of social changes in a captive chimpanzee community following the successful integration of two
568 adult groups. *American Journal of Primatology*, *75*(3), 254-266.
569 Schino, G., Rosati, L., & Aureli, F. (1998). Intragroup variation in conciliatory tendencies in captive Japanese
570 macaques. *Behaviour*, *135*(7), 897-912.
571 Schino, G., Troisi, A., Perretta, G., & Monaco, V. (1991). Measuring anxiety in nonhuman primates: effect of
572 lorazepam on macaque scratching. *Pharmacology Biochemistry and Behavior*, *38*(4), 889-891.
573 Semple, S., Harrison, C., & Lehmann, J. (2013). Grooming and anxiety in Barbary macaques. *Ethology*, *119*(9),
574 779-785.
575 Troisi, A. (2002). Displacement activities as a behavioral measure of stress in nonhuman primates and human
576 subjects. *Stress*, *5*(1), 47-54.
577 Waitt, C., & Buchanan-Smith, H. M. (2001). What time is feeding?: How delays and anticipation of feeding
578 schedules affect stump-tailed macaque behavior. *Applied Animal Behaviour Science*, *75*(1), 75-85.
579 Wells, D. L. (2005). A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas.
580 *Applied Animal Behaviour Science*, *93*(1), 13-17.
581 Whitehouse, J., Waller, B. M., Chanvin, M., Wallace, E. K., Schel, A. M., Peirce, K., ... & Slocombe, K. (2014).
582 Evaluation of public engagement activities to promote science in a zoo environment. *PloS one*, *9*(11),
583 e113395.
584 Wyngaarden, J. B. (1992). Smith L. *Cecil textbook of medicine*, *19*.

585

586 **Figure Captions**

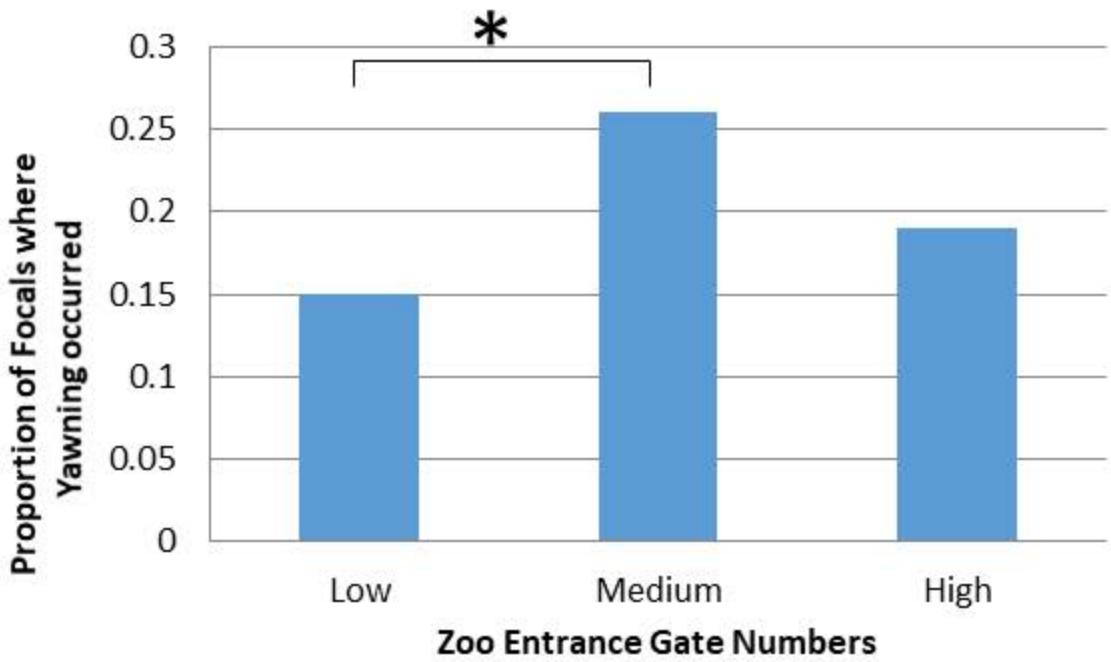
587 Figure 1 – The proportion of focal samples where the focal individual was seen to yawn when the Zoo
588 entrance numbers were low (0-1000), medium (1001-4000) and high (4001+). * denotes post-hoc GLMM
589 showed a significant difference (p=0.005).

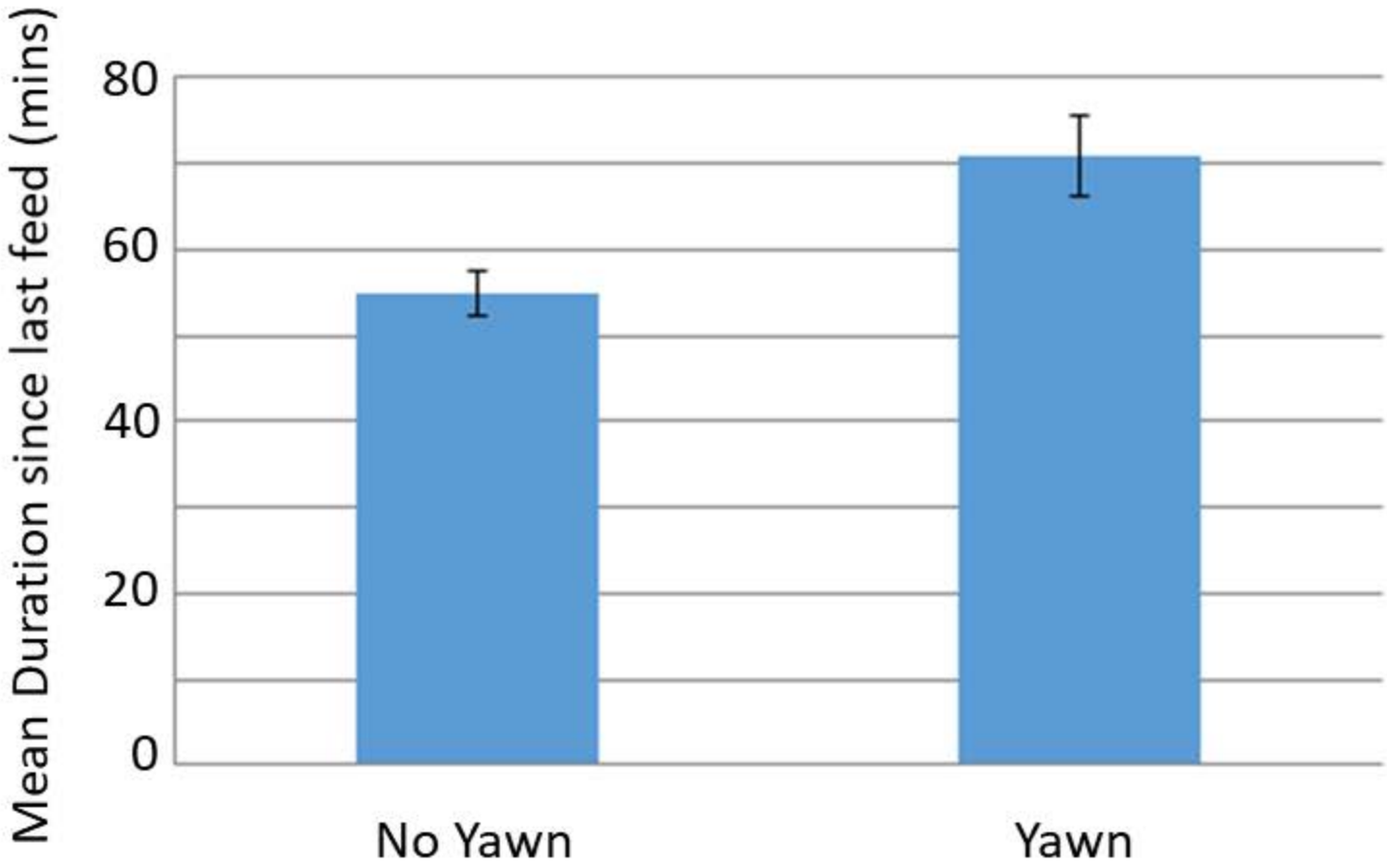
590

591 Figure 2- The mean duration in minutes from the last feeding event to the start of the focal samples where
592 the focal individual was seen to yawn and not yawn. Error bars show ± 1 *SEM*.

593

594 Figure 3- The median proportions of focal samples where R/R was observed for each of the nine BB individuals
595 throughout the integration process


*
0.3
0.25
0.2
0.15
0.1
0.05
0
Proportion of Focals where Yawning occurred
Low
Medium
High
Zoo Entrance Gate Numbers


Mean Duration since last feed (mins)
80
60
40
20
0
No Yawn
Yawn

Tables

Table 1. Variables included in GLMMs to answer each research question.

Research Questions: Are the abnormal or anxiety behaviours of chimpanzees affected by:	Dependent Variables (1 variable/ model)	N data points entered into model (N = individuals)	Independent Variable 1	Independent Variable 2	Independent Variable 3	Random Effect(s)
(i) number of visitors	Focal engaged in R/R? (Y/N)	68 (N = 6 individuals known to engage in R/R)	The level of visitor numbers present in the zoo on that day (low, medium and high)	N/A	N/A	Chimp Identity
	Focal scratched? (Y/N)	474 (N = 18)				
	Focal yawned? (Y/N)	474 (N = 18)				
(ii) visitor behaviour	Focal engaged in R/R? (Y/N)	68 (N= 6 individuals known to engage in R/R)	If a visitor used flash photography (Y/N)	If a visitor banged on the window of the focal pod (Y/N)	If a child screamed (Y/N)	Chimp Identity
	Focal scratched? (Y/N)	474 (N = 18)				
	Focal yawned? (Y/N)	474 (N = 18)				
(iii) involvement in grooming events	Focal engaged in R/R? (Y/N)	68 (N= 6 individuals known to engage in R/R)	Whether the focal animal received or gave grooming at any time during the focal sample (Y/N)	N/A	N/A	Chimp Identity
	Focal scratched? (Y/N)	474 (N = 18)				
	Focal yawned? (Y/N)	474 (N = 18)				
(iv) duration since being fed -	Focal scratched? (Y/N)	358 (N = 18)	The interval between previous	N/A	N/A	Chimp Identity

scratching and yawning	Focal yawned? (Y/N)	358 (N = 18)	feeding time and start of focal period			
(iv) duration since being fed - R/R	Focal engaged in R/R? (Y/N)	51 (from the 6 individuals known to engage in R/R)	Interval between the most recent and previous feeding event and the start of the focal period	N/A	N/A	Chimp Identity
(v) the type of food consumed	Focal engaged in R/R? (Y/N)	91 (from the 6 individuals known to engage in R/R)	The type of food recently provided (starchy vegetable, fruit or neither)	N/A	N/A	Chimp Identity ; Feeding event

Table 2. Results of the 15 GLMMs run to address each of the four research questions for each behaviour of interest (R/R, scratching and yawning). F, df and p values derived from likelihood ratio tests that compared the full model with a null model (intercept and random factors only), or the full model with a reduced model, designed to assess the contribution of a specific variable to explaining variation in the DV.

		R/R			**Scratching**			**Yawning**		
Are the abnormal or anxiety behaviours of chimpanzees affected by:	Independent Variables	F	df	p	F	df	p	F	df	p
(i) Visitor numbers	Total numbers of visitors in the zoo	2.07	2, 180	0.129	1.53	2, 471	0.217	**4.84,**	**2, 471**	**0.016**
(ii) visitor behaviour	Full Model	0.72	3, 64	0.546	1.56	3, 470	0.198	0.10	3, 470	0.395
	Children Screaming	1.25	1, 64	0.268	0.003	1, 470	0.957	*2.98*	*1, 470*	*0.085*
	Banging on Windows	0.04	1, 64	0.841	0.46	1, 470	0.496	1.67	1, 470	0.198
	Camera Flashes	0.97	1, 64	0.328	*3.59*	*1, 470*	*0.059*	0.003	1, 470	0.956
(iii) involvement in grooming events	Grooming	2.51	1, 181	0.115	1.04	1, 181	0.309	0.49	1, 181	0.486
(iv) length of time since being fed	Length of Time Between Feeding events	1.63	1, 49	0.208	0.08	1, 355	0.783	**5.30**	**1, 355**	**0.022**