1 **Exploration of potential triggers for self-directed behaviours and regurgitation and reingestion in zoo-**

2 **housed chimpanzees**

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

4 and Katie E. Slocombe [a]

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

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

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

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

9 e) During Data Collection: Department of Biological Anthropology, University of Cambridge, Pembroke Street,
10 Cambridge, CB2 3QG. Current Affiliation: University of Helsinki, Department of Social Sciences, Unioninkatu
11 35, 00014

12 **Corresponding Author:**
13 **Katie Slocombe**
14 **Ks553@york.ac.uk**
15 **01904 322905**

16
17

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.

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'

73 (Mallapur et al., 2005).

74 It is not just high levels of SDBs that can occur in response to captive environments; abnormal behaviours

75 can arise, which are defined as a set of behaviours that are performed either solely in captivity or at a much

76 higher level than in the wild and are thought to be indicators of poor welfare (Birkett and Newton-Fisher,

77 2011; Mason, 1991; Bloomsmith et al., 2019). A recent study found that 64% of sampled chimpanzees

78 within the United States had been seen to engage in at least one type of abnormal behaviour in the past

79 two years (Jacobson, 2016), which shows that these behaviours are prevalent within captivity. One

80 abnormal behaviour that has been observed across a range of captive primates is regurgitation and

81 reingestion (R/R). It has been observed in chimpanzees (Baker and Easley, 1996), bonobos (*Pan paniscus*)

82 (Miller and Tobey, 2012), gorillas (Akers and Schildkraut, 1985; Hill, 2009), and lion-tailed macaques

83 (Mallapur et al., 2005). The behaviour is defined as the voluntary movement of food from the stomach or

84 the oesophagus into the hand, the mouth or on to a substrate followed by the consumption of the

85 regurgitant (Gould and Bres, 1986). It is similar to rumination, a human abnormal behaviour that can lead

86 to serious health issues, such as oesophageal strictures, ulcers, reflux, oesophagitis, intestinal obstruction,

87 oesophageal motor disorders and pulmonary aspiration (Wyngaarden et al., 1992; Hill, 2009). To date no

88 single trigger for R/R has been identified; rather multiple factors have been suggested. Life history and

89 demographic factors have been shown to influence the likelihood of individuals engaging in R/R. A recent

90 survey of chimpanzees living in research facilities in the United States, conducted by Bloomsmith et al.

91 (2019), found that adults over the age of 40 were more likely to engage in R/R than adults 12- 39 years old,

92 possibly because older adult animals may have lived through a time when the welfare levels within

93 research centres were not as high as today. In addition, non-mother reared/non-wild born individuals living

94 in pairs were more likely to engage in R/R than mother reared or wild born chimpanzees, possibly due to

95 the lack of mother rearing. It has been shown that being deprived of mother rearing can cause emotional

96 trauma and lead to the development of abnormal behaviours (Kalcher et al., 2008).

97 Indeed, rumination in humans has been linked to anxiety (Landis and Lambroza, 2001), which suggests that

98 this could also be a more immediate trigger for the behaviour in animals. Previous research has suggested

99 other immediate triggers for R/R may include boredom (Baker, 1997, 2004), diet (Morgan et al., 1993; Lukas

100 et al., 2014) and visitor presence and behaviour (Mallapur et al., 2005; Wells, 2005). Taken together, it seems

101 a range of factors may influence engagement in this behaviour, with some suggesting a link to current or

102 previous stress, but a lack of consistency across studies and populations highlights a need for further

103 research. A better understanding of the causes of R/R may enable effective interventions to be implemented,

104 which would be valuable as R/R is likely to be negatively perceived by zoo visitors (Ackers and Schildkraut,

105 1985) and could affect the educational potential of the exhibit by giving false impressions of the species

106 (Carlstead, 1998; Ironmonger et al., 1992; Ackers and Schildkraut, 1985).

107 In order to reduce anxiety-related and abnormal behaviours in zoo-living animals, it is first important to

108 understand the aspects of this captive environment that may increase stress or abnormal behaviour. Zoo

109 visitors are a potential source of anxiety, in terms of their numbers and behaviour. For example, mandrills

110 (*Mandrillus sphinx)* exhibit higher levels of leg/hair pulling, stereotyped locomotion and masturbation in the

111 presence of high visitor numbers (Chamove et al., 1988). In terms of visitor behaviour, in a multi-species

112 study at Sacramento zoo it was found that active groups of visitors (where at least one individual attempted

113 to attract an animal's attention), regardless of size, induced more locomotion and audience-directed

114 behaviours than passive groups, although the authors do not state if they believed that was a sign of a

115 positive or negative welfare change (Mitchell et al., 1992). Previous studies have found, however, that the

116 activity or noise level of visitors negatively affects the behaviour of captive primates (Chamove et al., 1988;

117 Birke, 2002). If the presence or behaviour of visitors in zoos has a negative effect on animal welfare then

118 more research is needed into exactly which behaviours and numbers of visitors causes these effects and how

119 they can be minimised.

120 The type and availability of food in captive environments are very different from that found in most species'

121 natural environments (Oftedal and Allen, 1996) and, therefore, feeding regimes could be a potential source

122 of stress and/or triggers for R/R. Fruit and starchy vegetables increased R/R rates in laboratory chimpanzees

123 and zoo-housed gorillas (Morgan et al., 1993; Lukas et al., 2014). In addition, increasing the amount of time

124 since eating has also been linked to higher R/R rates in chimpanzees (Baker and Easley, 1996). This may be

125 due to longer periods between feeds violating anticipated feeding times, as delays to expected feeds

126 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

181   involved in dyadic grooming (including roles in these interactions; self-grooming was not recorded) whilst

182   the frequency of yawning, scratching and engaging in R/R were recorded. To be counted as separate events,

183   an inter-event period of at least 2 seconds was required for all behaviours (e.g. two yawns 1 second apart

184   would be counted as 1 yawn; two scratches 5 seconds apart would be counted as 2 events). Due to the large

185   number of samples where zero events were recorded, the frequency data we collected was extremely

186   skewed and transformation was ineffective. Therefore, we converted these behavioural measures into

187   categorical variables where the behaviour was either present or absent within a focal sample period.

188   Examination of the visitor number data through Q-Q plots and the acquisition of significant Shapiro-Wilk tests

189   of normality indicated that this variable was also not normally distributed, even after transformation.

190   Therefore, this variable was also converted into a categorical variable. Total visitor numbers within the zoo

191   (data based on gate numbers provided by Edinburgh Zoo) were categorised into low (0-1000), medium (1001-

192   4000) and high (4000+) visitor numbers. The category boundaries for this variable was chosen as they gave a

193   roughly equal distribution of data in each category.

194   The keepers provided detailed records of the time, type and quantities of food given to the chimpanzees on

195   a daily basis. Food data were categorised based on methods used by Plowman (2013) into starchy vegetables,

196   fruit or other. If feeds were given that contained multiple food types, each type of food was categorised

197   separately so there were multiple data points for that feed. To account for taking multiple samples from

198   some feeding events, feeding event was entered as a random factor into our statistical models. Before data

199   analysis was undertaken, it was noted that only six of the 18 chimpanzees were regularly seen to engage in

200   R/R and the majority of these events (16 out of a total of 27 observed during study period; 59.3%) happened

201   within 40 minutes of the most recent feed. For these reasons, the data for all analysis of R/R came from just

202   those six chimpanzees and focal samples that occurred within 40 minutes of a keeper feeding event.

203   **2.2 Data Analysis**

204   *2.2.1 Statistical Analysis*

205   General Linear Mixed Models (GLMMs) with a binomial error structure and a logit link were used to

206   investigate the influence of categorical and continuous explanatory variables on whether or not the

207   chimpanzees displayed the behaviours in question. Individual identity was included as a random factor to

208   address the issue of pseudoreplication due to each individual contributing multiple data points to the

209   analyses. Likelihood ratio tests were run for full models and to determine the contribution of each variable

210   in the model. If a factor that explained significant variation in a dependent variable contained three

211   categories, post-hoc GLMMs were run, each containing two of the three categories within the factor. All tests

212   were run using SPSS v.21 with an alpha value of .05, but with Bonferroni corrected alpha levels of .017 applied

213   to post hoc tests.

214   Table 1 shows each of the research questions and the breakdown of the variables included in each of the

215   GLMMs that were run in order to answer each of those questions. For question (iv) that related to R/R, as

216   the majority of R/R events were observed occurring when food was available during or shortly before the

217   focal observation period, we looked at if the duration between the most recent feed (within the last 40

218   minutes from the focal period) and the previous feed affected the occurrence of R/R. The sample was limited

219   to sessions where the previous feeding opportunity was known (i.e. sessions where the previous feed was

220   the day before were omitted to control for opportunistic overnight eating).

221   ------Table 1 ----

222   **2.3 Results**

223   *2.3.1 Descriptive Results*

224   The raw frequencies of scratching, yawning and R/R events can be seen in Table S2. The proportion of focal

225   samples (N = 474) where the focal individual was observed (i) scratching was 0.62, (ii) yawning was 0.20 and

226   (iii) engaging in R/R was 0.04. For R/R, if we just examined data from the six individuals who had been known

227   to regularly engage in R/R prior to the study period, they were observed to engage in R/R in 0.15 of their

228   total 183 focal samples or 0.28 of the 68 focal samples within 40 minutes of a feed. Although the likelihood

229   of yawning and scratching occurring was higher in the six individuals who regularly engaged in R/R compared

230   to the 12 individuals who did not regularly engage in R/R, this pattern was not significant (Median proportion

231   of focal samples where yawning occurred for R/R individuals = 0.23 (IQR = 0.20) and for Non R/R individuals

232   = 0.16 (IQR = 0.06); Mann Whitney U test U = 24.50, p = .279; Median proportion of focal samples where

233   scratching occurred for R/R individuals = 0.63 (IQR = 0.12) and for Non R/R individuals = 0.56 (IQR = 0.30);

234   Mann Whitney U test U = 27.50, p = .425)

235

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

Visitor numbers in the zoo did not explain a significant amount of variation in whether R/R or scratching

behaviour occurred (Table 2) but did explain a significant amount of variation in whether the chimpanzees

yawned (Table 2). Post-hoc GLMMs revealed that a significantly higher proportion of focal samples contained

yawning when there were a medium number of visitors in the zoo compared with a low number of visitors

$(F = 8.13$ (1, 402), $p = 0.005$; Figure 1). The likelihood of the focal chimpanzee yawning was not different for

any other pairwise comparisons in the post-hoc GLMMs (see table S3).

------Table 2 -----

------Figure 1 -----

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

None of the different types of potentially disruptive visitor behaviours explained a significant amount of

variation in whether or not the chimpanzees engaged in R/R (Table 2). Overall visitor behaviour did not

explain a significant amount of variation in whether or not chimpanzees scratched (Table 2), however, when

individual factors within the model were examined, there was a trend for a higher proportion of focal samples

to contain scratching when flash photography was used (0.70) than when it was absent (0.59; Table 2). Again,

overall visitor behaviour did not explain a significant amount of variation in whether or not chimpanzees

yawned but there was a trend for a higher proportion of focal samples to contain yawning when children

screamed (0.26) than when they did not (0.18; Table 2).

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

Receiving or giving grooming at any time during the focal period did not affect whether or not the

chimpanzees engaged in R/R, scratched or yawned (Table 2).

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

The amount of time from the most recent feeding event influenced the likelihood of yawning, which

increased as interval between feeding increased (Figure 2), but not the likelihood of scratching or R/R (Table

2).

----Figure 2-----

262 *2.3.6 Does the type of food consumed affect the likelihood of Regurgitation and Reingestion?*

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

264 **2.4 Discussion**

265 The main finding of this study is that, contrary to the predictions, few of the potential environmental triggers

266 we examined significantly affected the occurrence of SDBs or R/R within this group of chimpanzees. One

267 factor of the captive environment we did find to contribute to increases in SDBs was the duration between

268 feeding events. In the wild, chimpanzees spend 6.68 hours per day foraging or eating (Leonard and

269 Robertson, 1994) whilst in captivity this is greatly reduced (Chamove et al., 1982) and can mean that there

270 are long periods of time between feeding events. Our results show that when the chimpanzees have to wait

271 longer to eat they are more likely to yawn. Apart from one visitor talk feed which occurs at a standard time

272 each day, the keepers aimed to feed at irregular intervals to prevent anticipatory behaviours, and it is unlikely

273 that yawning is an anticipatory response in this group. Automatic feeders that release food at specific times

274 or random intervals could help negate this issue and reduce potential stress in captive chimpanzees.

275 Several studies have shown that high visitor numbers can negatively affect behaviour (Birke, 2002) leading

276 us to predict that having a high number of visitors would lead to an increase in SDBs. We found no evidence

277 of visitor numbers affecting scratching or R/R, but, in line with our prediction, we did find that there was a

278 higher proportion of focal samples where the focal animal yawned when there were medium zoo gate

279 numbers (1001 to 4000 people) compared to low number of visitors (0-1000). However, contrary to the

280 prediction, yawning was not more likely when high rather than medium or low numbers of visitors were in

281 the zoo. This result is unexpected and shows that further research into other associated factors, such as

282 duration of visitor stay at enclosure windows and visitor noise levels, are required to establish what is driving

283 this effect. Although visitor behaviour did not explain a significant amount of variation in whether SDBs or

284 R/R occurred, there were trends for yawning being more likely when children were screaming and scratching

285 being more likely when flash photography was used. This highlights these visitor behaviours as potentially

286 problematic, and future research with more groups and individuals is needed to investigate these factors

287 further.

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

289 contrasts with work on long-tailed macaques (Schino et al., 1988), crested black macaques (Aureli and Yates,

290 2010), and bonobos (Miller and Tobey, 2012), but supports previous findings in barbary macaques (*Macaca*

291 *sylvanus*) (Semple et al., 2013). Semple et al. suggest that when the macaques terminated a grooming event

292 it may have led to an increase in anxiety, which counter-acted the positive, anxiety reducing effect of

293 grooming that would have been expected to lead to a reduction in scratching.

294 Previous research has suggested that the type of food given to the chimpanzees (Morgan, 1993) and

295 increased time between feeds (Baker and Easley, 1996) can affect R/R behaviour, however, this was not

296 found to be the case with this group of animals. Although we found no evidence that R/R was linked to

297 potentially stressful concurrent events, we had an excellent opportunity to track whether large scale events

298 affected the frequency of this behaviour.

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

300 **3.1 Aims and Research Questions**

301 Given the lack of immediate factors influencing R/R in this group, we wanted to investigate longer term

302 influences on this behaviour. More specifically we aimed to examine if the translocation and integration into

303 a new social group and major diet changes affected the rates of R/R. We also examined the stability of R/R

304 rates from 2009 to 2015. Analyses were focussed on the nine of the 11 BB chimpanzees who were integrated

305 into the Edinburgh group in 2010, were still alive in 2015 and who had relatively high levels of R/R behaviour

306 at their previous facility. These nine individuals included all six individuals who were observed to engage in

307 R/R in study one. In addition, given that anecdotal reports from keepers and researchers indicated that the

308 original EZindividuals did not engage in R/R prior to the arrival of the BB group, we wanted to test whether

309 this behaviour spread through social learning. Many chimpanzees in captivity are moved between facilities

310 for breeding programmes so it is important to understand if this is a socially learnt negative behaviour, as

311 coprophagy has been suggested to be (Hopper et al., 2016).

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

313 1) Did the introduction of the BB individuals to Edinburgh Zoo cause their R/R rates to increase? It was

314 predicted that R/R rates would increase during the introduction between the two groups of individuals as

315 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).

343   3) July 2010 to February 2015 at Edinburgh Zoo. Much of the data from this time period came from University

344   of York researchers working on independent research projects in 2010-11, as well as long-term observational

345   data collection that was introduced in 2012 by KS. All long-term researchers conducting independent

346   research projects at Budongo Trail contributed to the data set, once they had passed an identification test to

347   ensure they could reliably identify all individuals. Detailed instructions were given to researchers and they

348   submitted data regularly for checking by KS or EW, so they received feedback on their data collection, but no

349   formal measures of interobserver reliability were taken. 10-minute focal samples were conducted where all

350   instances of the focal engaging in R/R were recorded, along with details of which other chimpanzees were in

351   the same pod as the focal animal and which of those were within 3 meters of the focal individual at the time

352   of each R/R event. Data on changes to diets and the dates of the integration process were obtained from

353   the keepers. 3612 focal samples were collected (602 hours).

354   In order to make all three sets of data comparable, each focal observation was scored for whether or not at

355   least one R/R event occurred in the 10-minute time period and only complete focal periods were considered.

356   **3.3 Data Analysis**

357   *3.3.1 Are the changes to R/R related to the integration process?*

358   Individual proportions of focal observations where R/R was observed per month for the BB individuals were

359   calculated. These monthly proportions were averaged for three time periods: pre-integration of the BB

360   individuals (May to September 2009), during the integration (May to July 2010) and immediately post

361   integration (August to December 2010). A Friedman test (N= 9) was used to compare the average rates of

362   R/R for the three time periods.

363   *3.3.2 Are the changes to R/R related to diet changes?*

364   The monthly proportion of focal observations where R/R was observed for the BB individuals, were used to

365   compare the average R/R rates of the three months before and after a major diet change. On 20th October

366   2010 an additional 50kg of grapes, pears and mangos, 15kg of apples and four loaves of white bread were

367   included in the weekly diet of the chimpanzees. Individuals were observed for a minimum of 18 focal samples

368   (three hours) during each three- month period. A Wilcoxon test (N= 9) was used to compare the mean of the

369   proportions of observations where R/R occurred in each three-month period before and after the diet

370   change.

371   *3.3.3 Have the proportion of focals where R/R was observed changed over time?*

372   For each year, from 2009 to 2015, a yearly proportion of focals where R/R was observed for each individual

373   was calculated by averaging the available monthly proportions in each year. These values for the 9 BB

374   individuals were then averaged to create a group annual mean. The relationship between time (year) and

375   R/R proportions was examined using a Kendall's-tau correlation, due to the small sample size.

376   *3.3.4 Have the EZ individuals socially learnt the behaviour from the BB individuals?*

377   We wanted to establish if observing the BB chimpanzees engaging in R/R lead to the EZ individuals adopting

378   the behaviour. We calculated the total number of R/R events that the BB individuals were recorded as

379   engaging in. We also determined the number of these events where at least one EZ chimpanzee was present

380   within 3 metres of a BB individual, from where they could have observed the behaviour closely. The data

381   used for this came from August 2010 – 2015, once the BB had been fully integrated into the group. We then

382   calculated the total number of times each of the EZ individuals were recorded to have engaged in R/R to see

383   if the behaviour was adopted by those animals.

384   *3.3.5 Statistical analysis*

385   All tests run were two-tailed with alpha level set at 0.05 and Bonferroni corrected to p= 0.017 for post hoc

386   tests. Wilcoxon Signed Ranks, Friedmans and Kendall's-tau tests were run using SPSS v.21. Effect sizes (*d and*

387   *r*) were calculated using an online tool (http://www.uccs.edu/~lbecker/). When using Cohen's *d* as an effect

388   size, .80 is considered a large effect, .50 a medium sized effect, and 0.20 a small effect (Cohen, 1992). *r* was

389   used as an effect size for non-parametric Wilcoxon Signed Rank tests, in which 0.50 or above is a large effect,

390   above 0.30 a medium effect and 0.10 a small effect (Pallant, 2007).

391   **3.4 Results**

392   *3.4.1 Are the changes in R/R related to the integration process?*

393   There were significant differences between the proportions of observations where R/R occurred pre-, during

394   and post integration (Friedman X^2(2) = 9.60 N= 9, p=0.008; Figure 3). Using Bonferroni corrected alpha levels,

395   post-hoc Wilcoxon signed ranks tests show that the proportions of R/R were significantly higher in the pre-

396   integration than during the post-integration period (Z= -2.38, p=0.017; *r*= 0.24). There were trends for the

397 proportions of R/R being higher during pre-integration than in the integration period (Z= -2.24, p=0.025;

398 r=0.61) and in integration than post-integration (Z= -2.20, p=0.028; r=0.50). Figure 3 illustrates that all

399 individuals observed to engage in R/R showed a decrease over the integration process and that this pattern

400 was not driven by a single individual.

401 ----Figure 3 -----

402 *3.4.2 Are the changes in R/R related to diet changes?*

403 R/R proportions were not significantly higher after the diet change (median = 0.073; IQR = 0.13) than before

404 (median = 0.071; IQR = 0.16; Wilcoxon Z= -0.41 N= 10 p=0.686; *r*= 0.16).

405 *3.4.3 Has the proportion of focals where R/R was observed changed over time?*

406 There was a trend for the proportion of focals where R/R was observed decreasing over the period from 2009

407 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

408 individuals and indicates that all individuals contribute to the overall group decrease rather than one

409 individual driving it.

410 *3.4.4 Have the EZ individuals socially learnt the behaviour from the BB individuals?*

411 We found that the EZ chimpanzees were within 3 metres of 89 R/R events and the BB chimpanzees were

412 recorded to engage in R/R a total of 160 times from August 2010-2015, which means that the EZ chimpanzees

413 were in proximity to 55.6% of all observed R/R events. Despite this, no EZ individual was seen to engage in

414 R/R themselves more than four times between August 2010 and July 2013 (see Table S5). The number of R/R

415 events by the EZ individuals was low and sporadic and no events were recorded after July 2013.

416 **3.5 Discussion**

417 It was predicted that observations of R/R would increase during the introduction between the two groups of

418 individuals as this was believed to be a stressful time for the animals. However, R/R proportions were

419 significantly higher before the introduction. This suggests that either the integration process did not involve

420 as much negative stress as assumed or more likely, given the convergent results of study 1, R/R is not a

421 response to current stress levels. It is possible that R/R is related to boredom (Baker, 1997; 2004) and that

422 the cognitive challenge presented to the BB chimpanzees by the introduction to a new physical and social

423 environment may have reduced their boredom and, therefore, their proportions of focal samples where R/R

424   was observed. Previous studies have found that the provision of foraging related enrichment (Baker, 1997)

425   and increased human caretaker interaction (Baker, 2004) has led to reductions in R/R rates. We therefore

426   recommended that further research investigating the link between boredom and R/R should be undertaken.

427   In October 2010, the diet of the chimpanzees changed and the amount of fruit given weekly increased. Based

428   on the results of Morgan et al. (1993) it was predicted that this would lead to an increase in R/R. However,

429   comparing the proportions of R/R for three months on either side of this diet change showed there was no

430   significant difference, however, this could have been because rates were already low before the change (only

431   8/743 samples prior to the diet change contained an R/R event). There were other small changes to the diet

432   of these chimpanzees from April 2010 onwards but we lacked sufficient data to examine three months prior

433   to and after each of these changes. It is possible, therefore, that each of these small changes may have

434   contributed to the overall reduction in R/R within the BB individuals.

435   By looking longitudinally at the R/R performed by the chimpanzees at Edinburgh Zoo we have been able to

436   identify that the proportion of the BB individuals' focal periods where R/R was observed has a trend for

437   reducing over time, which suggests an improvement in their welfare. Some BB individuals (Pearl, Edith, Eva

438   and Heleen) were no longer observed engaging in R/R by 2015. The design of Budongo Trail and being part

439   of the large, socially complex group of chimpanzees is the most probable cause of the reduction of R/R rates

440   since 2009 in the BB individuals. The fact that six of the animals still occasionally engage in R/R is likely due

441   to the persistent nature of the behaviour and is possibly a form of coping strategy, similar to stereotypical

442   behaviours (Higham et al., 2009). In humans, the same behaviour, known as rumination (Nakanishi and

443   Anderson, 1982), has been linked to periods of distress in individuals of average intelligence but the

444   behaviour is very difficult to eradicate (Nakanishi and Anderson, 1982). Mulder et al. (2016) found that

445   feeding a higher fibre diet did reduce rates of R/R in the chimpanzees at Amersfoort Zoo but the behaviour

446   did not disappear, suggesting the behaviour had become a habit. Although we do not know the full history

447   of the BB animals during their time in the medical testing facility, it is likely that the experience may have

448   been stressful and this is where they first performed R/R. Once established as a behaviour pattern, it may be

449   difficult to eliminate, hence why the BB individuals still perform the behaviour, albeit at much lower levels.

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

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

4. Conclusions

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

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.

531 Kalcher, E., Franz, C., Crailsheim, K., & Preuschoft, S. (2008). Differential onset of infantile deprivation

532 produces distinctive long-term effects in adult ex-laboratory chimpanzees (Pan troglodytes). *Developmental*

533 *Psychobiology: The Journal of the International Society for Developmental Psychobiology*, *50*(8), 777-788.

534 Landis, B., & Lambroza, A. (2001, March). A respiratory biofeedback solution for the rumination syndrome.

535 In *Biological Psychology* (Vol. 56, No. 1, pp. 79-80)., NETHERLANDS: ELSEVIER SCIENCE BV.

536 Leonard, W. R., & Robertson, M. L. (1994). Evolutionary perspectives on human nutrition: the influence of

537 brain and body size on diet and metabolism. *American Journal of Human Biology*, *6*(1), 77-88.

538 Lukas, K. E., Bergl, R., Ball, R., Kuhar, C. W., Lavin, S. R., Raghanti, M. A., ... & Dennis, P. M. (2014).

539 Implementing a low-starch biscuit-free diet in zoo gorillas: The impact on health. *Zoo Biology*, *33*(1), 74-80.

540 Maestripieri, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: displacement activities as an

541 indicator of emotions in primates. *Animal Behaviour*, *44*(5), 967-979.

542 Mallapur, A., Sinha, A., & Waran, N. (2005). Influence of visitor presence on the behaviour of captive lion-

543 tailed macaques (*Macaca silenus*) housed in Indian zoos. *Applied Animal Behaviour Science*, *94*(3), 341-352.

544 Mellor, D. J., & Beausoleil, N. J. (2015). Extending the 'Five Domains' model for animal welfare assessment

545 to incorporate positive welfare states. *Animal Welfare*, *24*(3), 241-253.

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

547 Miller, L. J., & Tobey, J. R. (2012). Regurgitation and reingestion in bonobos (*Pan paniscus*): Relationships

548 between abnormal and social behavior. *Applied Animal Behaviour Science*, *141*(1), 65-70.

549 Mitchell, G., Tromborg, C. T., Kaufman, J., Bargabus, S., Simoni, R., & Geissler, V. (1992). More on the

550 'influence' of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science*, *35*(2), 189-

551 198.

552 Morgan, L., Howell, S. M., & Fritz, J. (1993). Regurgitation and reingestion in a captive chimpanzee (*Pan*

553 *troglodytes*). *Lab Animal*, 22:42-45.

554 Mulder, I., van der Meer, R., de Vries, H., & Sterck, E. H. M. (2016). The relationship between diet change and

555 regurgitation and reingestion in captive chimpanzees. *Journal of Zoo and Aquarium Research*, *4*(4), 196.

556 Nakanishi, D. A., & Anderson, D. R. (1982). Behavioral Treatment of Psychogenic Vomiting Among Children-

557 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.

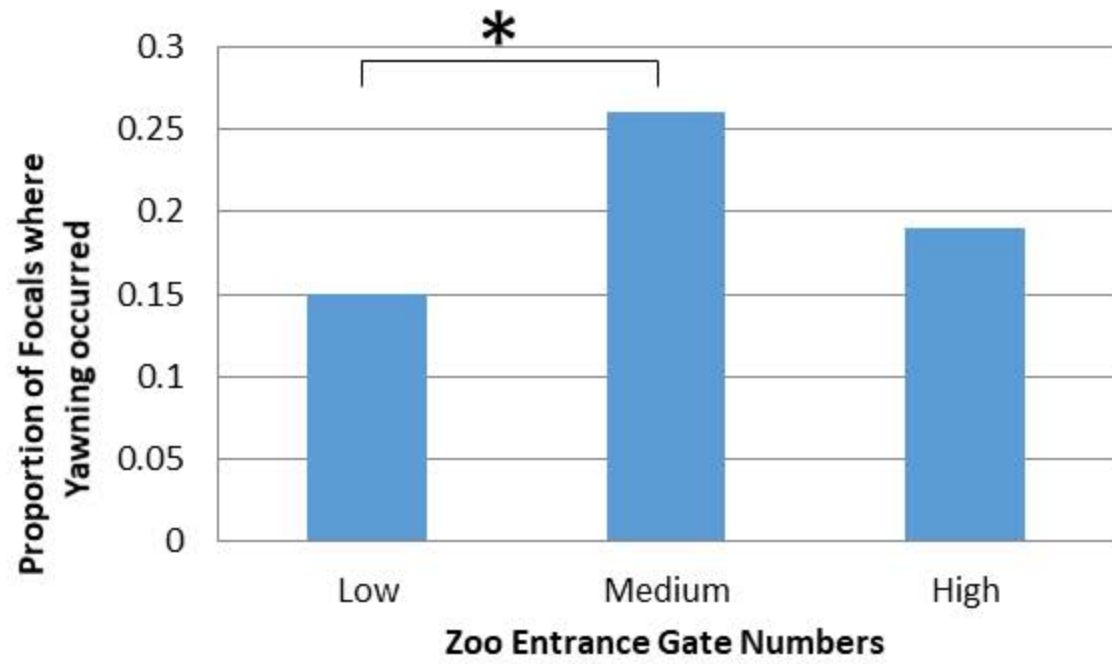584 Wyngaarden, J. B. (1992). Smith L. *Cecil textbook of medicine*, *19*.

585

Figure Captions

Figure 1 – The proportion of focal samples where the focal individual was seen to yawn when the Zoo entrance numbers were low (0-1000), medium (1001-4000) and high (4001+). * denotes post-hoc GLMM showed a significant difference (p=0.005).
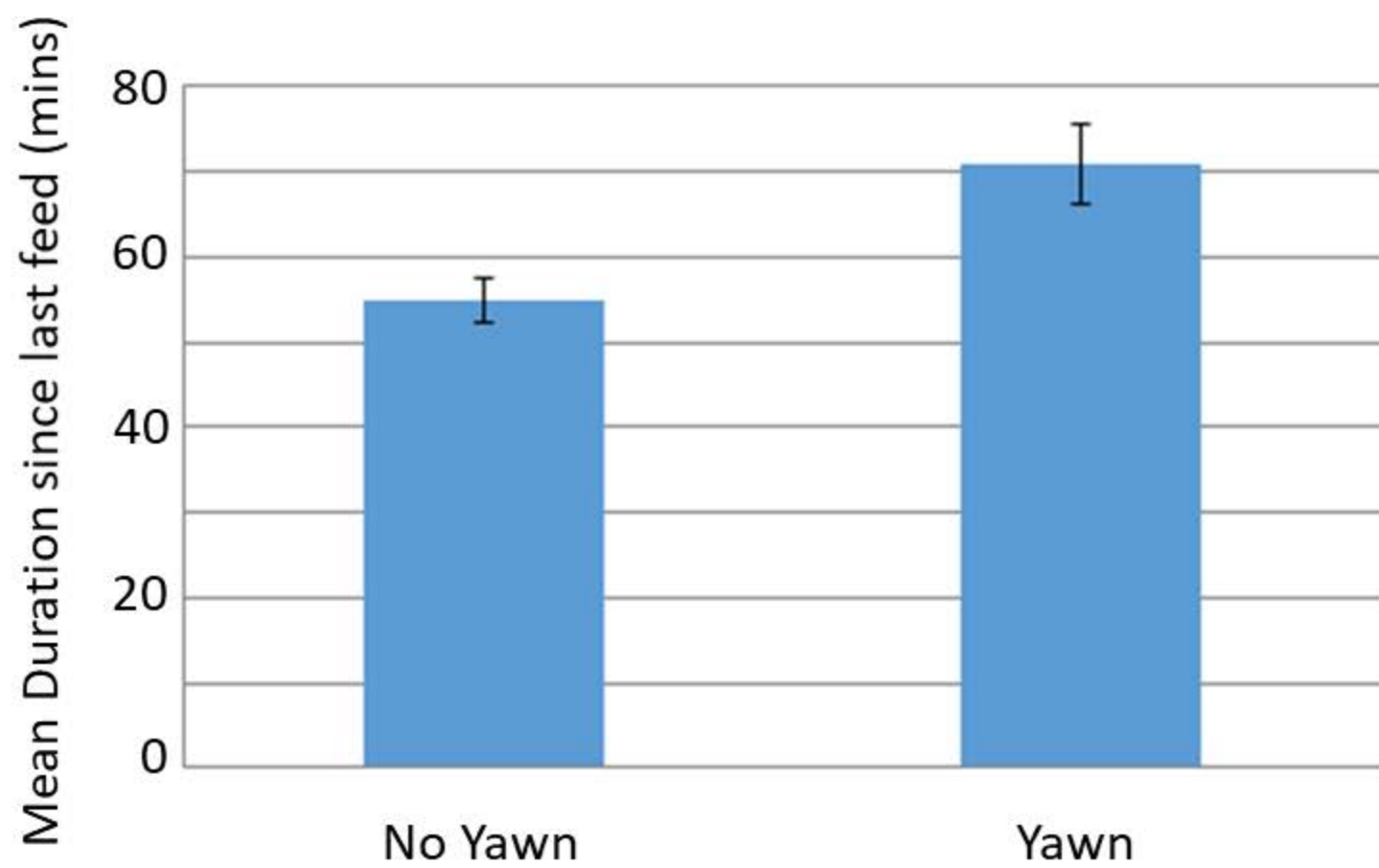
Figure 2- The mean duration in minutes from the last feeding event to the start of the focal samples where the focal individual was seen to yawn and not yawn. Error bars show ± 1 *SEM*.

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

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.

Are the abnormal or anxiety behaviours of chimpanzees affected by:	Independent Variables	R/R			Scratching			Yawning		
		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**