

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

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

20 **Abstract**

21 The unique challenges faced by animals living in zoos can lead to the production of anxiety-related  
22 behaviours. In this study we aimed to understand what specific factors may cause chimpanzees to display  
23 these behaviours. In non-human primates, displacement behaviours, such as self-scratching and yawning,  
24 are considered markers of anxiety and stress, and Regurgitation and Reingestion (R/R) is considered an  
25 abnormal behaviour with negative consequences for physical health. We examined the possible triggers of  
26 R/R, scratching, and yawning in a group of zoo-housed chimpanzees and followed this up with an analysis of  
27 long-term data to examine further aspects of R/R behaviour. In the first study we conducted focal  
28 observations on 18 adult chimpanzees at Edinburgh Zoo, UK, in addition to all occurrence sampling of visitors  
29 using flash photography, screaming and banging on the glass in the exhibit. 158 hours of data were analysed  
30 and Generalised Linear Mixed Models revealed that yawning was significantly more likely if there was a long  
31 period of time since the last feed and when there were moderate numbers of visitors in the zoo. There were  
32 trends that yawning was more likely to occur if children screamed and that scratching was more likely to  
33 occur if visitors used flash photography. R/R occurred most often within 40 minutes of a feed, but was not  
34 affected by the inter-feed interval preceding that feed, positive or negative social interactions, or visitor  
35 numbers or behaviour. As there was no obvious daily trigger for R/R, an analysis of long-term data (2009 to  
36 2015) was conducted to investigate if social or dietary factors affected rates R/R over a larger timescale. It  
37 was found that R/R rates in the months before a significant diet change were not different from R/R rates in  
38 the months after, but it was found that R/R rates decreased over the five-year period. Lastly, we found no  
39 evidence that the introduction of individuals engaging in R/R lead to resident chimpanzees habitually  
40 adopting the behaviour, despite considerable opportunities to observe it. These findings have implications  
41 for welfare interventions aimed to reduce R/R and/or anxiety behaviours in captive populations and for the  
42 translocation of individuals that are known to engage in R/R between groups.

43  
44 **Keywords**

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

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## 48 **1. Introduction**

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

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

68 Previous research has indicated that a range of factors can increase anxiety levels in zoo-housed primates,  
69 which is manifested in elevated rates of self-scratching and yawning. When not given enrichment, high visitor  
70 numbers were associated with high rates of scratching in two groups of captive gorillas (*Gorilla gorilla gorilla*)  
71 (Carder and Semple, 2008). In an Indian zoo, where the lion-tailed macaques were often 'taunted' by visitors,  
72 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; Bloomsmithe 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 Bloomsmithe 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).

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

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

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

154 **2.1 Methods**

155 *2.1.1 Study Site*

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

163 *2.1.2 Subjects*

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

169 *2.1.3 Data collection*

170 Data collection occurred over two study periods; 13<sup>th</sup> March 2014 to 8<sup>th</sup> July 2014 and 6<sup>th</sup> January 2015 to 2<sup>nd</sup>  
171 March 2015. Ethical approval was obtained from the Animal Welfare Ethical Review Board of the Dept. of  
172 Biology, University of York. Twenty minute focal samples (Altmann, 1974) were carried out on all 18 adult  
173 individuals within the group (mean = 27.8 samples/individual; range = 20-57). No more than three  
174 consecutive focal samples, lasting an hour in total, were collected within each 'pod' within the enclosure. No  
175 animal was observed more than once each day and individuals with the least focal minutes were  
176 preferentially chosen as focal animals from those available in the pod. Only complete focal samples where  
177 the individual was observed for the full 20 minutes were included in the analysis, making a total of 474 focal  
178 samples (158 hours). During the focal period, we used one/zero sampling to record if visitors used flash  
179 photography (Y/N), percussed (banging, tapping etc.) on the windows of the enclosure (Y/N) and if children  
180 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)

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*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 EZ individuals 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.

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

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

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

### 329 **3.2 Methods**

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

333 1) May to September 2009 at Beekse-Bergen Safari Park. Data were collected by SK and students using 10-  
334 minute long focal samples (Altmann, 1974) to record the duration of time spent engaging in R/R by the focal  
335 individual. Prior to data collection, inter-observer reliability test between SK and each student showed >90%  
336 identical data coding. 836 focal samples were collected (139.3 hours). 836 focal samples were collected  
337 (139.3 hours).

338 2) March to October 2010 at Edinburgh Zoo (pre-, during and immediately post integration of BB and EZ  
339 groups) 10-minute focal samples were conducted and the frequency of R/R within each sample period  
340 recorded. Data were collected by ESH and 2 research assistants, with interobserver reliability tested at 2 time  
341 points and agreement on presence or absence of R/R completely reliable ( $R = 1.0$ ). 1133 focal samples were  
342 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 20<sup>th</sup> 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 ( $\tau_b = -0.62$ ,  $n = 9$ ,  $p = 0.051$ ). 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

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.

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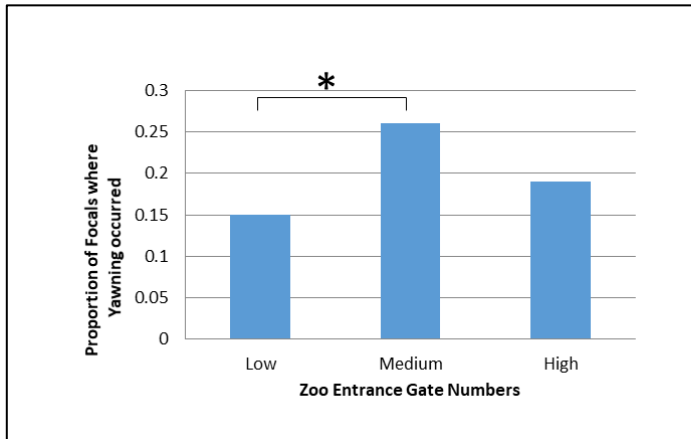
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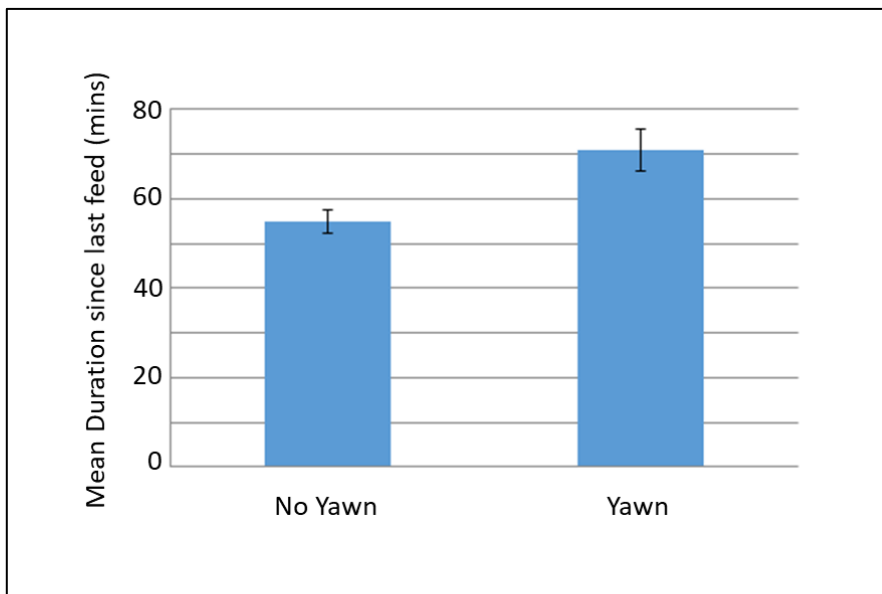
585

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



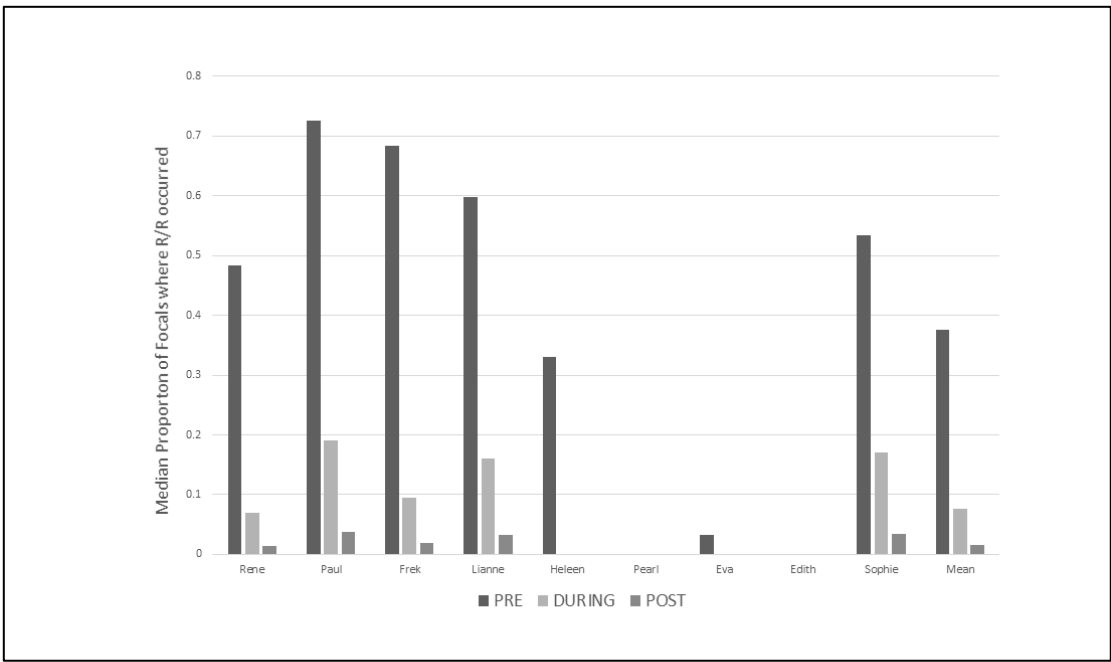
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590 Figure 2- The mean duration in minutes from the last feeding event to the start of the focal samples where  
591 the focal individual was seen to yawn and not yawn. Error bars show  $\pm 1$  SEM.



592

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



595

596



Tables

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

<b>Research Questions: Are the abnormal or anxiety behaviours of chimpanzees affected by:</b>	<b>Dependent Variables (1 variable/ model)</b>	<b>N data points entered into model (N = individuals)</b>	<b>Independent Variable 1</b>	<b>Independent Variable 2</b>	<b>Independent Variable 3</b>	<b>Random Effect(s)</b>
(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	N/A	N/A	Chimp Identity

	Focal scratched? (Y/N)	474 (N = 18)	during the focal sample (Y/N)			
	Focal yawned? (Y/N)	474 (N = 18)				
(iv) duration since being fed - scratching and yawning	Focal scratched? (Y/N)	358 (N = 18)	The interval between previous feeding time and start of focal period	N/A	N/A	Chimp Identity
	Focal yawned? (Y/N)	358 (N = 18)				
(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

600

601

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

	Independent Variables	R/R			Scratching			Yawning		
		F	df	p	F	df	p	F	df	p
Are the abnormal or anxiety behaviours of chimpanzees affected by:										
(i) Visitor numbers	Total numbers of visitors in the zoo	2.07	2, 180	0.129	1.53	2, 471	0.217	<b>4.84,</b>	<b>2, 471</b>	<b>0.016</b>
(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	<b>5.30</b>	<b>1, 355</b>	<b>0.022</b>

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