JZAR JOURNAL OF ZOO AND AQUARIUM RESEARCH
www.jzar.org

Research article

The relationship between diet change and regurgitation and reingestion in captive chimpanzees

Iris Mulder[1], Raymond van der Meer[2], Han de Vries[1] and Elisabeth H.M. Sterck[1,3*]
[1]*Animal Ecology, Utrecht University, Utrecht*
[2]*Dierenpark Amersfoort, Amersfoort*
[3]*Ethology Research, Biomedical Primate Research Centre, Rijswijk*
**Correspondence: Elisabeth H.M. Sterck; e.h.m.sterck@uu.nl*

Keywords:
abnormal behaviour, boredom, fibre, inactivity, self-directed behaviour, stress

Article history:
Received: 8 December 2015
Accepted: 4 October 2016
Published online: 3 November 2016

Abstract
Captive chimpanzees regularly show abnormal behaviour, including regurgitation and reingestion (R/R). R/R may have several causes, among them a suboptimal diet. For this reason, the effect of a diet change towards a more fibre-rich diet on R/R was studied in the Amersfoort Zoo chimpanzee group comprising 15 individuals. In addition, the relationship with self-directed behaviour, inactivity level and temperature, proxies of the alternative factors stress, boredom and crowding, were studied. Measures of stress and boredom did not show any correlation to R/R behaviour. The new diet did result in less R/R. However, the data could not conclusively dismiss temperature as a factor or confound in the reduction of R/R. Still, the R/R rate in three individuals that showed most R/R did not concur with temperature, countering an effect of temperature on R/R. Individuals that showed R/R in the study period still showed this behaviour several years later, suggesting that R/R may not be related to current welfare but possibly become a habit, where stress and R/R become dissociated and the behaviour persists in improved conditions and over time. This study shows that diet change can contribute to a reduction in R/R, yet this may not be due to the change of diet quality, but to the change in diet as such. The change in diet was not able to abolish R/R behaviour entirely for these chimpanzees.

Introduction

Captive chimpanzees (*Pan troglodytes)* often show abnormal behaviour, which is defined as behaviour not present at all or only in low frequencies in wild chimpanzees (Broom and Johnson 1993). This type of behaviour may indicate that the animal is having welfare problems (Barnett and Hemsworth 1990; Mason et al. 2004, 2007), which makes it an important subject for research. The range of abnormal behaviour in captive chimpanzees is large, including regurgitation and reingestion (R/R) (Birkett and Newton-Fisher 2011). Furthermore, the causes of abnormal behaviour are diverse, ranging from long-term effects of unnatural rearing conditions and the individual's psychological status to short-term effects such as feeding regime (Mason et al. 2004, 2007). Short-term effects in particular may be regulated by management changes. The potential for reducing abnormal behaviour through management would be highly valuable for optimising husbandry.

R/R is an abnormal behaviour where animals voluntarily stimulate the retrograde movement of food or fluids from the oesophagus or stomach to the mouth, hand or another substrate and subsequently reconsume the substance (Lukas 1999). It is comparable to the rumination syndrome in humans (Lukas 1999), but should not be compared to rumination as part of the digestive process in herbivores (Hill 2009). R/R has been observed in captivity in macaques (*Macaca mulatta*), baboons (*Papio cynocephalus*), *vervet monkeys* (*Chlorocebus pygerythrus*), proboscis monkeys (*Nasalis larvatus*), siamangs (*Symphalangus syndactylus*), gibbons (*Hylobatis spp.*), orangutans (*Pongo pygmaeus*), lowland gorillas (*Gorilla gorilla*), bonobos (*Pan paniscus*) and chimpanzees (Baker and Easley 1996; Miller and Tobey 2012). It has negative effects on health, since it may cause teeth to deteriorate and negatively affect the oesophagus (Hill 2009). For this reason, elimination of this behaviour is desirable for the wellbeing of animals showing R/R. To find a way to decrease or eliminate R/R, it is important

to focus on the possible causes. To date four have been proposed: feeding practices that differ from the wild, boredom due to unenriched housing conditions, psychological problems resulting from stress, and crowding during winter conditions (Lukas 1999; Struck et al. 2007).

First, feeding practices can strongly influence the behaviour of captive primates. The diet of wild chimpanzees is diverse and consists mainly of wild plants (Wrangham et al. 1991). These are less digestible and have higher fibre content than domesticated fruit, vegetables and typical primate pellets (Crissey and Pribyl 1997). The high digestibility of the captive chimpanzee diet may leave an unsatisfied feeling. Moreover, highly enjoyable food may promote R/R (Lukas 1999). In captive gorillas, implementing a high fibre and low starch diet or removing milk from the diet reduced the occurrence of R/R (Lukas et al. 1999; Bergl et al. 2014). Therefore, a high fibre diet may reduce R/R in chimpanzees.

Second, when housing conditions are insufficient, the animals may start performing abnormal behaviour to cope with their relatively unchallenging captive situation. Lack of enrichment to fill their relatively high amount of spare time may lead to abnormal behaviour due to boredom. Simply adding straw bedding, corn, seeds and peanuts to the enclosures of captive chimpanzees, providing long-lasting foraging opportunities, significantly reduces or, for some individuals, even eliminates R/R (Baker 1997). A very different type of enrichment, playing naturalistic sounds in the enclosure, has also proved to decrease R/R behaviour in gorillas (Robbins and Margulis 2014). In addition, reducing boredom is suggested to be effective in decreasing abnormal behaviour (Barnett and Hemsworth 1990; Celli et al. 2003). This predicts that more time spent inactive may increase R/R.

Third, psychological issues are thought to influence the occurrence of abnormal behaviour, including R/R (Nash et al. 1999; Honess and Marin 2006). R/R may be affected by stress. Social stress, because of negative social behaviour within the group, has been shown to influence R/R, as the behaviour increases when other animals are acting aggressively (Miller and Tobey 2012). Given these observations we hypothesise that more stressed individuals will exhibit more abnormal behaviour.

Fourth, crowding due to weather conditions may affect captive chimpanzee behaviour: in bad weather individuals may mainly or only use crowded inside enclosures, leading to limiting housing conditions and social stress. Accordingly, the anxiety rate of chimpanzees is significantly higher in a crowded situation than under less crowded circumstances (Aureli and De Waal 1997). This converges with the second and third potential causes: unfit housing conditions or psychological problems. Taken together these findings lead to the prediction that due to crowding in cold weather conditions R/R could be higher than in warmer conditions. However, in wild chimpanzees higher temperatures render the animals less active: they rest more (Kosheleff and Anderson 2009) and may be more bored. This leads to the assumption that in cold weather conditions R/R could be lower than in warmer conditions.

Overall, it is clear that the causes of R/R are still partially uncertain. The aim of this study was to investigate whether the change to a diet with high fibre content reduced the rate of R/R in a group of captive chimpanzees at the Amersfoort Zoo in which several individuals performed R/R. To include other potential causes, the relationship between abnormal behaviour and stress, inactive behaviour and weather conditions was determined as well.

Table 1. Individual information on each of the subjects observed.

Name	Sex	Birth year	Born in	R/R 2011	R/R 2015#
Belle	F	1977	Captivity	+	+
Bibi	F	1996	Captivity		
Chura	F	1997	Captivity		
Ituri	F	2003	Captivity	+	Died
Jet	F	1970*	Wild		Died
Karibuna	M	2000	Captivity		
Kokkie	F	1966*	Wild	+	+
Kumi	M	2001	Captivity		
Mike	M	1965*	Wild	+	
Sanne	F	1989	Captivity		
Sjors	F	1966*	Wild	+	+
Sonja	F	1964*	Wild	+	Died
Sylvia	F	1974*	Wild		Died
Willy	F	1991	Captivity	+	+
Wingu	M	2009	Captivity		

Birth year: * estimated. Rearing history of wild born individuals was not known; all captive born individuals were mother-reared.
Observational data from Lisa Brink and Anne Marijke Schel, spring 2015.

Methods

Subjects and housing

The behaviour of 15 captive chimpanzees living in one group at Amersfoort Zoo was investigated. The group consisted of four males and 11 females, varying from one to 47 years of age (Table 1). Most individuals were born in captivity and were reared by their mother. The six oldest animals were born in the wild and caught at a young age, their rearing type is unknown.

The chimpanzees were housed in an enclosure with an indoor and an outdoor compartment. The indoor compartment measured 96m^2 and was 4m high; the outdoor compartment measured 475m^2 and was 4.2m high. In addition, seven night enclosures (4m^2 and 2m high) were available. The animals were shut in these enclosures each night, but they were generally not used during the day.

Diet and diet change

The chimpanzees' main diet consisted of old world primate pellets, fruits and vegetables, such as carrots, onions and kiwis. The chimpanzees were fed five times per day. The first meal, around 0815, consisted of two or three pieces of vegetables and a piece of fruit per animal, fed by hand. The second meal, at 0900, consisted 5 kg of vegetables for the whole group in the outdoor compartment. The third meal, at 1200, consisted of 4.5 kg of pellet for the whole group. The fourth meal, at 1400, consisted of a vegetable snack. The fifth meal, at 1630, consisted of two pieces of vegetables and one piece of fruit per animal. The type of vegetable or fruit varied daily. Water was available ad libitum.

The diet change involved the substitution of one type of old world primate pellets with another type. Prior to the onset of the study, the animals had been fed the old diet for several years. The pellets were changed halfway through the observation period to a pellet with lower energy and higher fibre content. The old diet, Primate Pellet PT (2512), contained 16.865 kJ/kg energy and 2.2% fibre. The new diet consisted of Nutrazu® Primate Maintenance Biscuit. This pellet contained 11.346 kJ/kg energy and 9.3% fibre. The new pellets also differed from the old pellets in size, shape and structure. The choice of old and new diet was the initiative of

Table 2. Description of R/R and behaviours considered self-directed behaviour (SDB: Baker 1997, Hill 2009).

Behaviour	Specific action	Description
R/R		Voluntarily stimulating the retrograde movement of food or fluids from the oesophagus or stomach to the mouth, hand or another substrate and subsequently reconsuming the substance
Self-directed behaviour (SDB)	Nose rub	Strokes under/on nose with arm or hand
	Scratch	Self-touching involving the ends of the digits, potentially including movement of the shoulder joint
	Yawn	Open mouth and expose teeth in a gaping movement
	Autogroom	Bout of grooming own fur with one's mouth or hand(s)

Dierenpark Amerfoort; the manufacturers of the primate pellets were not involved.

Observations

Observational data were collected by IM over 64 days between 27 January and 6 May 2011, using focal observations of all 15 individuals between 0930 and 1600. From 27 January to 11 March 2011 the animals ate the old diet; from 14 March to 6 May 2011 they ate the new diet. For both periods the subjects were observed for 32 days. Each animal was observed daily three times for five minutes, resulting in 16 observational hours per subject. A schedule changed daily ensured that observations were balanced over the day, to counter effects of daytime on behaviour. Before and after the diet change, the same schedule was used. During observations, the chimpanzees most often had access to both their indoor and outdoor compartments.

During focal observations, using time sampling on every minute on the minute, fifteen data points were collected per day, recording active behaviour, i.e. feeding, moving and social behaviour, and inactive behaviour, i.e. sleeping and resting. The percentage of inactive behaviour in all time samples was calculated.

In addition, both stress behaviour, measured as self-directed behaviour (SDB: Maestripieri et al. 1992), and abnormal behaviour were recorded continuously during the focal observations (Table 2). SDB was the summed number of nose rubs, scratching, yawning and the number of auto-grooming bouts (a new bout was recorded when auto-grooming stopped for ≥ 30 seconds: cf. Maestripieri et al. 1992; Aureli and de Waal 1997; Leavens et al. 2004). For SDB and R/R, the rate per hour was calculated.

Observational data on the persistence of R/R in this group were available for spring 2015. These data were collected by Lisa Brink and Anne Marijke Schel as part of a larger study. Not all individuals present in 2011 were also present in 2015 (see Table 1). Data on R/R were collected during focal observations (around 13 h of data per individual) and ad libitum observations of the complete group (70 h for the whole group).

Weather conditions

The diet change took place on 14 March 2011, when in the Netherlands the winter turns into spring. The weather conditions were determined on a daily basis, and measured by temperature in (0.1° C) and the durations of sunshine and rain (in 0.1 h).

Data analysis

The abnormal behaviour R/R was not normally distributed, therefore non-parametric tests to look for relationships between SDB, diet change, origin of birth and R/R were performed. Non-parametric statistical analyses were conducted using SPSS Inc. 22.0 for Windows.

Data were analysed with linear mixed models (using the package *lme4* (Bates et al. 2014) in R 3.2.2) to test the effects of temperature and diet on inactive behaviour and SDB. For each behaviour, three models were compared: mm0 included the by-individual random intercepts effect on the behaviour and the by-individual random slopes effects of diet and temperature on the behaviour; mm1 added to mm0 the effect of temperature; mm2 added to mm1 the fixed effect of diet. Because our main interest was in finding a possible effect of diet on the two types of behaviour after controlling for temperature, we first added temperature and then diet to the model. We used the likelihood ratio approach to test the significance of each of the added effects on the behaviour. After applying the arcsine (square root) transformation on the variables 'inactive' and 'SDB', visual inspection of the residuals plotted against the predicted values from mm2 revealed no strong deviation from normality and homoscedasticity.

Tests were two-tailed, with alpha set at 0.05.

Results

Prevalence of R/R

In a group of 15 chimpanzees, seven individuals showed R/R. The rate of R/R varied from 1 R/R per 16 h of observation (rate: 0.06/h) to 129 R/R per 16 h (rate: 8.06 /h) and was on average 32 R/R per 16 hours (rate: 1.99/h). Of the six wild born chimpanzees, four performed R/R, while of the nine captive-born chimpanzees, two performed R/R. There was no significant association between origin (wild or captive-born) and presence of R/R (n=15; Fisher's exact test for 2 by 2 cross table, two-tailed p = 0.31)

Self-directed behaviour and R/R

The relationship between SDB and R/R was determined in both 32-day periods. In both periods, the individuals' rate of SDB and their R/R rate were not significantly correlated (Period 1: Spearman correlation coefficient=0.310; n=15; p=0.26; period 2: Spearman correlation coefficient=0.017; n=15; p=0.95).

The effect of temperature and diet change on inactive behaviour and SDB

The diet change took place on 14 March 2011, when in the Netherlands the winter turns into spring. Indeed, the weather was colder in the period with the old diet than with the new (Mann Whitney U-test (MWU-test): U=62.5; n=64, p<0.001), the duration of sunshine was shorter (MWU-test: U=293; n=64, p=0.003) and the duration of rain higher (MWU-test: U=374; n=64, p=0.026). Therefore, effects of the diet change may be confounded by different weather conditions.

The effects of temperature and diet change on behaviour were investigated with linear mixed model analyses (Table 3). The comparison between mm0 and mm1 was significant for inactive behaviour, indicating that at higher temperatures individuals were significantly more often inactive than at low temperatures. The lack of a significant difference between mm1 and mm2 indicates that the change from the old to the new diet did not significantly affect inactive behaviour, after statistically controlling for temperature. A similar pattern was found for SDB: the linear mixed models of SDB showed a significant difference between mm0 and mm1, but not

Table 3. Linear mixed models of effect of temperature and diet on two behaviours: inactive behaviour and self-directed behaviour (SDB), both of which arcsine transformed. Three models were compared: mm0 included the by-individual random intercepts effect on the behaviour and the by-individual random slopes effects of diet and temperature on the behaviour; mm1 added to mm0 the effect of temperature; mm2 added to mm1 the fixed effect of diet. Pr(>Chisq) is the P-value of the added effect.

Model	df	logLik	Deviance	Chisquare	df	P(>Chisq)
Inactive behaviour						
Mm0	8	-683.0	1366.0			
Mm1	9	-676.1	1352.2	13.71	1	0.00021
Mm2	10	-675.2	1350.4	1.78	1	0.18
Self-directed behaviour						
Mm0	8	-676.7	1353.4			
Mm1	9	-682.0	1364.0	10.62	1	0.0011
Mm2	10	-682.8	1365.7	1.67	1	0.20

Models:
Mm0: BEHAVIOUR ~ (1 + diet + temp| indiv)
Mm1: BEHAVIOUR ~ temp + (1+ diet + temp | indiv)
Mm2: BEHAVIOUR ~ diet + temp + (1 + diet + temp | indiv)

between mm1 and mm2. This indicates that at higher temperatures individuals showed less SDB than at low temperatures, but that the diet change did not affect SDB, after statistically controlling for temperature. In sum, the behaviour of the chimpanzees was significantly affected by temperature, but a possible effect of diet on the behaviour, after controlling for temperature, could not be detected.

The effect of temperature and diet change on R/R

The possible effect of diet change on abnormal behaviour was determined by comparing the individual summed instances of R/R in the 32-day old diet period with the corresponding values in the 32-day new diet period. Including in this comparison the seven chimpanzees that performed R/R, we found that R/R was significantly lower in the new diet period compared with the old diet period (Wilcoxon signed ranks matched pairs test: n=7, exact two-tailed p=0.031; Figure 1).

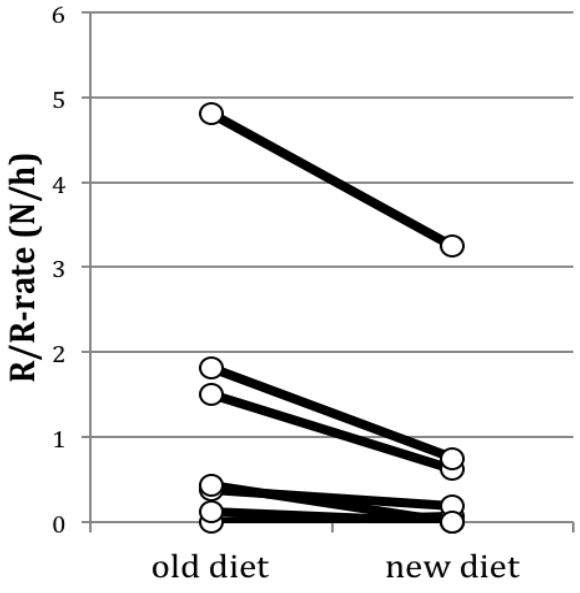

Figure 1. The rate of R/R (N/h) in the 32-day periods of the old and the new diet.

The relationship between temperature and R/R could only be investigated in three animals, due to the high number of days without observations of R/R for the other chimpanzees. To determine whether the observed change of R/R was consistent with the change in average temperature within the periods with old and new diet, the data for the three individuals that exhibited most R/R were subdivided into four 16-day periods: two of the old diet and two of the new diet. The average temperature in the four periods was respectively 4.2, 2.7, 8.6 and 12.7 ^{o}C. These descriptive data indicate that R/R was lowest in the first period with the new diet and that the R/R in the second period of the new diet was comparable to the two periods with the old diet (Figure 2). The incidence of R/R does not seem to follow the average temperature in the four periods.

Persistence of R/R

While in 2011 the R/R rate was reduced by the new diet, only in two of the individuals was it completely absent in the period with the new diet (Figure 1). We were interested in the long-term effects as well. During a new observational study in 2015, four of the individuals observed in 2011 still showed R/R, two individuals had died and one, who had a low rate of R/R in 2011, did not show it in 2015 (Table 1). In addition, the eight individuals that did not show R/R in 2011 also did not show it in 2015. Therefore, R/R seems to be a persistent behaviour once individuals show it.

Discussion

We investigated whether a diet change from a standard to a higher fibre diet reduced R/R in the captive group of chimpanzees at Amersfoort Zoo. The incidence of R/R was lower in the period with the new fibre-rich diet than in the period with the old diet. Additionally, the diet change did not significantly affect inactive behaviour or SDB, after statistically controlling for the confounding variable temperature. Moreover, individual differences in SDB rate did not correlate with the incidence of R/R. This suggests that a high fibre diet may reduce R/R in captive chimpanzees.

Effect of high fibre diet

One of the foremost predictions of this research was that the new high fibre diet would cause the animals to decrease their R/R behaviour. Indeed, the change from the standard to the high fibre diet concurred with a significantly reduced amount of R/R in 6 out of the 7 chimpanzees that performed this behaviour. Alternatively, R/R may result from re-ingesting highly enjoyable food (Lukas 1999), and the reduced R/R when eating a fibrous diet suggests that this may form a less preferred diet.

However, descriptive data indicate that when the results were divided into four time periods, R/R was low in the period directly after the diet change, and not in the last 16-day observation period. This suggests that the decrease in R/R behaviour was a temporary effect. This may be caused by the newness of the diet, suggesting that it is dietary variation, and not the type of diet, that reduced R/R. This is also consistent with the persistence of R/R reported in this group: when the feeding regime concerns only long-term dietary changes, it may not be effective in reducing R/R. Alternatively, familiar food may be more enjoyable food, thereby promoting R/R (cf. Lukas 1999). Indeed, chimpanzees may prefer familiar food (Remis 2002). This proposition remains to be further explored, for example by studying whether R/R is more prevalent after ingesting preferred than non-preferred food. Overall, the

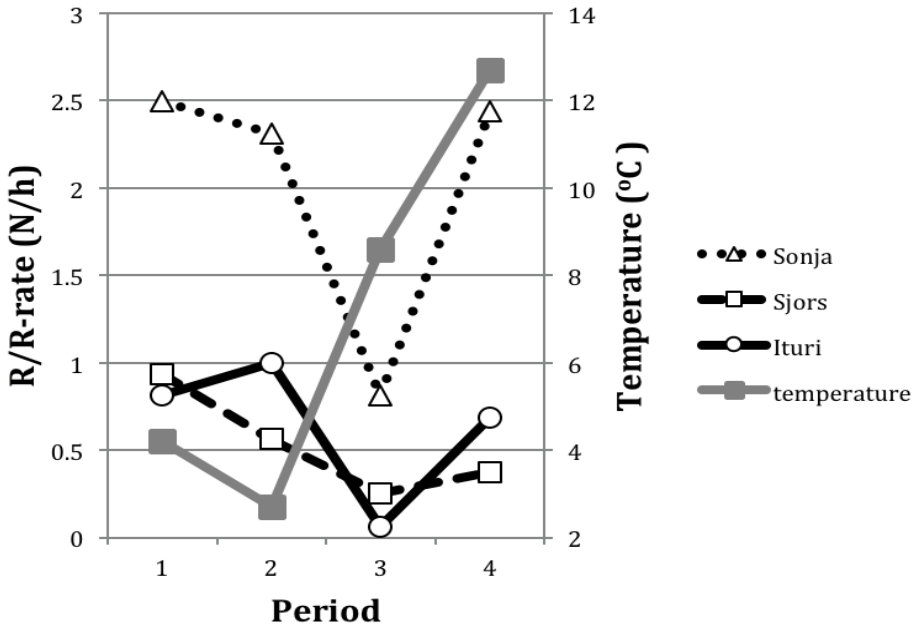

Figure 2. The rate of R/R (N/h) of three individuals that showed most R/R measured in four 16-day periods: two in the period of the old and two in the period of the new diet. The average temperature per period is plotted in grey.

proposition that consistent dietary variation may reduce R/R in the long run should be further explored. This may be similar to the effect of feeding enrichment techniques that regularly change the diet, which have previously been shown to be a successful method of reducing R/R in captive primates (Baker 1997; Lukas 1999; Bloomsmith et al. 2007).

Effect of boredom

It was expected that higher levels of boredom would result in an increase in R/R behaviour. In the period after the diet change the temperature was higher and at high temperatures the animals were more inactive. We expected that in this second period the animals would perform more R/R behaviour, yet we found the opposite: they performed less R/R. This suggests that boredom did not influence R/R. Alternatively, a (frequent) diet change may decrease a more long-term type of boredom. In this scenario, the diet change in itself may have functioned as a feeding enrichment technique to keep the animals stimulated. This possibility should be studied further.

Effect of stress

Abnormal behaviour may result from psychological problems such as current stress or reflect long-term effects such as suboptimal rearing conditions (Barnett and Hemsworth 1990; Mason et al. 2004, 2007). If stress affected R/R, a correlation with stress levels, measured by SDB, was expected. However, SDB and R/R did not correlate, indicating that stress does not result in R/R. Moreover, although SDB levels were lower in the spring than in the winter, consistent with going outside more often and reducing crowding (Aureli and De Waal 1997), they were not affected by the diet change.

Overall, the performance of R/R was not related to stress and thus may not be related to current welfare (Mason and Latham 2004). For example, when neural changes have occurred and the abnormal behaviour turns into an automatic process, R/R has most likely become a habit. Stress and R/R may become dissociated and thus R/R persists even in improved conditions and over time. Indeed, the persistence of R/R with the diet change, although at lower rates, and the persistence of R/R even four years later, indicate that it results from long-term effects on an individual's behaviour.

Effect of temperature/weather

Weather may have affected the reduction in R/R through its effect on crowding. Due to the relatively low incidence of R/R, it was not possible to directly correlate it with temperature. Yet the temperature was higher in the period with the new diet than in the period with the old diet. Therefore, the higher temperature may result in less R/R, as was also shown by other studies performed in wild chimpanzees (Kosheleff and Anderson 2009). Note that the temperatures in the Netherlands are typically much lower than for wild chimpanzees. However, the descriptive data indicate that temperature was not related to R/R in the three individuals that showed this behaviour most often. The current data cannot conclusively dismiss temperature or crowding as a factor in the reduction of R/R. A change in diet during a period with similar weather conditions would remedy this confound.

In conclusion, at first sight a change to a diet high in fibre seems to reduce R/R. Yet, although R/R is reduced, it does not abolish the behaviour and a few years later the individuals that showed R/R in the reported study still exhibited this behaviour. Therefore, R/R was not extinguished by the diet change. Moreover, descriptive data suggest that the effect of diet change may be only temporary and limited to a brief period after the introduction of the new diet. This suggests that it is not the high fibre content in the new diet but the change in diet that caused that reduction of R/R in chimpanzees. However, this remains to be investigated systematically. Long-term effects of diet change need to be monitored to determine their effectiveness.

Acknowledgements

We thank the caretakers of Dierenpark Amersfoort for their help during the research and commitment to the chimpanzees' welfare. We thank Lisa Brink and Anne Marijke Schel for sharing their observational data from 2015.

References

Aureli F., De Waal F. (1997) Inhibition of social behavior in chimpanzees under high-density conditions. *American Journal of Primatology* 41: 213–228.

Baker K.C. (1997) Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. *Zoo Biology* 16: 225–236.

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

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

Barnett J., Hemsworth P. (1990) The validity of physiological and behavioural measures of animal welfare. *Applied Animal Behaviour Science* 25: 177–187.

Bates D., Maechler M., Bolker B., Walker S. (2014) *lme4: Linear mixed-effects models using Eigen and S4.* R package version 1.1-7, <URL: http://CRAN.R-project.org/package=lme4>.

Bergl R., Ball R., Dennis P., Kuhar C., Lavin S., Raghanti M., Wensvoort J., Willis M., Lukas K. (2014) Implementing a low-starch biscuit-free diet in zoo gorillas: The impact on behavior. *Zoo Biology* 33: 63–73.

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

Bloomsmith M.A., Lambeth S.P. (1995) Effects of predictable versus unpredictable feeding schedules on chimpanzee behavior. *Applied Animal Behaviour Science* 44: 65–74.

Bloomsmith M.A., Marr M.J., Maple T.L. (2007) Addressing nonhuman primate behavioral problems through the application of operant conditioning: Is the human treatment approach a useful model? *Applied Animal Behaviour Science* 102: 205–222.

Broom D.M., Johnson K.G. (1993) *Stress and Animal Welfare.* Berlin: Springer Science and Business Media.

Celli M.L., Tomonaga M., Udono T., Teramoto M., Nagano K. (2003) Tool use task as environmental enrichment for captive chimpanzees. *Applied Animal Behaviour Science* 81: 171–182.

Crissey S.D., Pribyl L.S. (1997) Utilizing wild foraging ecology information to provide captive primates with an appropriate diet. *Proceedings of the Nutrition Society* 56: 1083–1094.

Hill S.P. (2009) Do gorillas regurgitate potentially-injurious stomach acid during 'regurgitation and reingestion?' *Animal Welfare* 18: 123–127.

Honess P., Marin C. (2006) Behavioural and physiological aspects of stress and aggression in nonhuman primates. *Neuroscience and Biobehavioral Reviews* 30: 390–412.

Kosheleff V.P., Anderson C.N. (2009) Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. *American Journal of Physical Anthropology* 139: 172–181.

Lukas K.E. (1999) A review of nutritional and motivational factors contributing to the performance of regurgitation and reingestion in captive lowland gorillas (*Gorilla gorilla gorilla*). *Applied Animal Behaviour Science* 63: 237–249.

Lukas K.E., Hamor G., Bloomsmith M.A., Horton C.L., Maple T.L. (1999) Removing milk from captive gorilla diets: the impact on regurgitation and reingestion (R/R) and other behaviors. *Zoo Biology* 18: 515–528.

Mason G.J., Latham N.R. (2004) Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? *Animal Welfare* 13 (supplement 1): 57–69.

Mason G., Clubb R., Latham N., Vickery S. (2007) Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science* 102: 163–188

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

Nash L.T., Fritz J., Alford P.A., Brent L. (1999) Variables influencing the origins of diverse abnormal behaviors in a large sample of captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology* 48: 15–29.

Remis M.J. (2002) Food preferences among captive western gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *International Journal of Primatology* 23: 231–249.

Robbins L., Margulis S.W. (2014) The effects of auditory enrichment on gorillas. *Zoo Biology* 33: 197–203.

Struck K., Videan E.N., Fritz J., Murphy J. (2007) Attempting to reduce regurgitation and reingestion in a captive chimpanzee through increased feeding opportunities: a case study. *Laboratory Animals* 36: 35–38.

Wrangham R.W., Conklin N.L., Chapman C.A., Hunt K.D. (1991) The significance of fibrous foods for Kibale Forest chimpanzees. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 334: 171–178.