'Regurgitation and reingestion' (R/R) in great apes: A review of current knowledge

S. P. HILL[1,2,*]

[1] *Department of Biological Sciences, University of Chester, Parkgate Road, Chester CH1 4BJ, United Kingdom, and* [2] *Department of Veterinary Medicine, University of Cambridge, Madingley Road, Cambridge CB3 0ES, United Kingdom*

E-mail: hill.s@chester.ac.uk

Right-hand running title: REGURGITATION AND REINGESTION (R/R) IN GREAT APES

Left-hand running title: CONSERVATION OF GREAT APES

Manuscript ID: IZY-17-025

Submitted: 4 December 2017

FOOTNOTE:

*Address for correspondence: Dr S. P. Hill, Department of Biological Sciences, University of Chester, Parkgate Road, Chester, CH1 4BJ, UK. hill.s@chester.ac.uk

ABSTRACT

Research indicates that regurgitation and reingestion (R/R) is a relatively common behaviour in zoo-housed great apes, with most work to date carried out on Western lowland gorillas *Gorilla gorilla gorilla* and Chimpanzees *Pan troglodytes*. It is an abnormal behaviour because great apes are not anatomically adapted to regurgitate their food as part of their normal feeding processes, and because this behaviour is not seen in members of the species living freely in the wild, in conditions that would allow a full behavioural range. In this article, I give an overview of the published literature on R/R in great apes, which suggests that this behaviour is probably multifactorial and may be linked to inappropriate feeding environments (e.g. in terms of nutritional composition of the diet and/or presentation of food), and possibly also social and other factors as well. A similar behaviour to R/R, known as rumination disorder, can also occur in another great ape species, humans, in whom it is classified as a feeding and eating disorder, and there are potential consequences to people's physical health as a result of oral acid. There have been no known studies to date to identify whether or not similar health consequences can occur in non-human great apes, but the regurgitant has been found to be significantly more acidic in gorillas than the food they ingested originally, meaning it is potentially injurious in non-human great apes. There is much that is not yet known about this behaviour and how to reduce or eliminate it when it does occur, as the research indicates that there are a range of factors involved, and these can vary by individual animal. More research into this behaviour is clearly needed to ensure that zoos and sanctuaries are providing the best possible care for these animals, and I make some suggestions for future research directions.

Key-words: abnormal behaviour; animal welfare; enrichment efforts; feeding environment; great apes; rumination disorder; sanctuary; social environment; zoo.

INTRODUCTION

Staff in modern zoos and sanctuaries increasingly recognize and address the need for a more evidence-based approach to animal husbandry and welfare (Melfi, 2009; Maple, 2014), with less of a reliance on the 'folklore husbandry' that has been adopted traditionally (Arbuckle, 2013). There has thus far been a taxa bias in research efforts in the field of zoo-animal welfare, with mammals (and, in particular, certain primates), being relatively well-studied compared with other taxa (Melfi, 2009). That said, there is still a lot more that needs to be understood, even for those primates about which we know a fair amount, if we are to provide optimal care for these animals when managed in zoos and sanctuaries. One of the areas that continues to challenge the level of care provided to great apes in zoos is the occurrence of a behaviour known as regurgitation and reingestion (R/R), earlier work on which has been reviewed previously by Lukas (1999) and Hill (2009), amongst others.

R/R is not part of the normal feeding mechanism in great apes (Hill, 2009). To date, there are no known reports of R/R occurring in wild (i.e. free-living) great apes (Cooper & Hull, 2017), or in wild-born sanctuary apes, but that is not to say that this behaviour might not be observed in animals in those settings in the future, if some aspect of their environment is not optimal (Hill, 2009). In contrast, R/R has been documented to occur in at least some individual animals, across nearly all zoo-housed species of great apes, including Chimpanzees *Pan troglodytes* (e.g. Baker & Easley, 1996; Baker, 1997; Herrelko *et al.*, 2015), Orangutans *Pongo* sp (e.g. Cassella *et al.*, 2012), Bonobos *Pan paniscus* (Miller & Tobey, 2012), and Western lowland gorillas *Gorilla gorilla gorilla* (e.g. Lukas, 1999; Lukas *et al.*, 1999; Hill, 2009; Fuller *et al.*, 2017), as well as some other primates (e.g. see Cassella *et al.*, 2012, and Miller & Tobey, 2012, for a brief review). A similar behaviour to R/R is also known to occur in people, another member of the great ape taxonomic family, which will be referred to later in this review.

The current article offers an overview of the existing knowledge on R/R, defining the behaviour, drawing comparisons with its human equivalent (American Psychiatric Association, 2013) where it is pertinent to do so, and investigating a range of possible motivational factors for R/R in zoo-housed great apes. I go on to make some suggestions for potential research areas, to help to inform future husbandry provision and promote positive welfare, which modern zoos are under increasing scrutiny to be proactive in (Hill & Broom, 2009; Rose *et al.*, 2014). Overall, the literature search revealed only a small number of papers published on R/R in recent years, with much of the (limited) work being a lot earlier (see review by Lukas, 1999).

DEFINING REGURGITATION AND REINGESTION (R/R)

R/R is classed as an abnormal behaviour in great apes (e.g. Pizzutto *et al.*, 2007); that is, it is a behaviour that differs in pattern, frequency or context from that which is shown by most members of the species under conditions that would allow a full behavioural range (Broom & Johnson, 2000; Hill & Broom, 2009), and the animals are not anatomically adapted to do R/R as part of their normal feeding mechanism (Hill, 2009). As in any behavioural study, it is important to describe the behaviour, and to define it unambiguously, to ensure the criteria can be understood and the same behaviours can be recognised easily by other observers (Martin & Bateson, 2007).

R/R in non-human great apes

Zoo-based studies have shown that among great apes that engage in R/R, regurgitation tends to occur shortly after eating and/or drinking and refers to a seemingly voluntary, effortless behaviour, characterized by the retrograde movement of food and/or drink from the oesophagus or stomach, to the mouth, hand or floor (e.g. see Lukas, 1999, for review), and in the absence of apparent retching or nausea. Reingestion occurs subsequently if the animal masticates and consumes the

regurgitated matter (Hill, 2009). R/R might also be carried out with more subtlety, such as being limited to a 'burp' (Hopper *et al.*, 2016) or a 'hiccup' type action (Gould & Bres, 1986; S.P. Hill, unpubl. data), followed by filled cheeks and mastication, and so the behaviour could potentially be easily missed if the observer is not well-practised in recognising it (Cassella *et al.*, 2012).

Despite its appearance, regurgitation is not the same as vomiting, although it is known that zoo visitors, researchers and caregivers who are unfamiliar with this behaviour can sometimes confuse the two. Unlike R/R, vomiting is an involuntary reflex behaviour brought about by autonomic activity and preceded by hypersalivation, contractions of abdominal muscles, retching and nausea (Strombeck, 1979), and tends to occur with some time-delay after eating (Cooper & Hull, 2017). In their paper on what they refer to as R/R in Bonobos, Miller & Tobey (2012) appear to be including self-induced, hand-assisted vomiting in their definition of this behaviour. In line with the rest of the literature on regurgitation and reingestion, I do not include hand-assisted 'regurgitation' in the behavioural definition of R/R, but that is not to say this behaviour should not be investigated further in its own right.

Some individual gorillas may also show pre-regurgitate or transitional behaviours (Akers & Schildkraut, 1985; Gould & Bres, 1986; Lukas *et al*., 1999; Hill, 2004; Fuller *et al.*, 2017). These are idiosyncratic, stereotyped behaviour patterns and are carried out immediately prior to regurgitating, such as repetitively sweeping away the substrate on the floor in a similar motion to foraging, rubbing the stomach for a few times with a clenched fist or drumming on the stomach, running a piece of straw or wood wool through the fingers repetitively, or repeatedly standing and tipping the head towards the floor, with buttocks pointing upwards, until regurgitation is achieved. Idiosyncratic behaviour actions are also part of the autism spectrum in people and are linked to self-stimulation, and can be a precursor of self-injurious behaviours (American Psychiatric Association, 2013; Rojahn *et al.*, 2016), but are not yet well understood in non-human great apes. Fuller *et al.* (2017) considered a bout of R/R in Western lowland gorillas to begin with the pre-regurgitate behaviours (if these occurred), but it would be useful if authors report these behaviours separately to the main onset of regurgitation in their analyses.

Pizzutto *et al*. (2007) have reported a stereotyped post-regurgitation/pre-reingestion behaviour pattern in a solitary-housed, off-exhibit male Gorilla at a Brazilian zoo. This male was observed to manipulate and separate the regurgitant into what appeared to be colour categories, and would always reingest the regurgitant in the same colour order, followed by salivary material, perhaps as a form of self-stimulation. The issue of positive reinforcement of R/R may be useful to consider, if it does have a self-soothing (calming) or self-stimulating function for (some) individuals (Pizzutto *et al*., 2007; Hill, 2009). Thus, R/R may be 'rewarding' to the animal in the short-term, when some aspect of their environment is not appropriate in meeting their biological needs, but it is important

to recognize that not all such behaviours are necessarily beneficial to the animal's welfare, and could even be potentially harmful (Broom & Johnson, 2000).

Rumination disorder in humans

In defining R/R in zoo-housed great apes, comparisons can be made with what appears to be a similar behaviour in humans, rumination disorder (American Psychiatric Association, 2013), previously known as human rumination syndrome (Hill, 2009). Arguably more is known about rumination disorder in humans than it is about R/R in non-human great apes, and so it can be useful to use the human literature as a reference point for R/R.

Rumination disorder is classified as a feeding and eating disorder (American Psychiatric Association, 2013), and the use of the word 'rumination' for these cases could perhaps be confusing, as humans (like other great apes) do not have a rumen (Hill, 2004). This 'rumination' cannot be linked to another medical condition, such as gastro-oesophageal reflux disease ('acid reflux' or GORD) or pyloric stenosis, and ideally these conditions should also be ruled out for non-human great apes that do R/R. Some human 'ruminants' self-report that the regurgitant tastes similar to the original food that was ingested, at least for the first few times it is regurgitated, before it takes on a more sour taste (Anon., pers. comm.). Likewise, one of the supporting diagnostic features that clinicians use in human cases is that infant 'ruminants' appear to gain satisfaction from the process of regurgitation and reingestion (American Psychiatric Association, 2013), supporting the suggestion that it does not taste or feel unpleasant to those doing it, and may perhaps be self-stimulating.

Rumination in people can occur because of a failed interaction with the caregiver (e.g. in human infants or adults with mental retardation) (Malcolm *et al.*, 1997; Wagaman *et al.*, 1998; Thame *et al.*, 2000), and this may be found to be a causal factor of R/R in some non-human apes, such as hand-reared individuals (Gould & Bres, 1986). Rumination has also been linked to a state of anxiety in otherwise mentally healthy adult people (Landis & Lambroza, 2001), which should be explored further in other apes, as it is known that captive environments can be sources of stress to animals (Pizzutto *et al.*, 2015).

In human 'ruminants', it is well documented that some clinical consequences can occur as a result of oral acid, such as dental erosion, motor disorders of the oesophagus, ulceration, oesophageal strictures and pulmonary aspiration (e.g. Monagas *et al.*, 2017; Thame *et al.*, 2000). It is known to be fatal in some human infants with this condition as a result of malnutrition and dehydration (Thame *et al.*, 2000). Possible consequences of oral acid in R/R in non-human great apes are considered in a later section of this review.

PREVALENCE OF R/R IN GREAT APES

It is widely acknowledged that R/R is a common behaviour in zoo-housed great apes, and most of the work to date has been done on Gorillas. The reader is directed to the review by Lukas (1999), which details earlier work in this area, albeit some repetition is made in the current article. Results of an unpublished survey, reported by its authors, on 206 gorillas housed in 56 North American zoos and primate centres, showed that a total of 68% (N=140) of those gorillas were known to do R/R (Akers and Schildkraut; 1985). Fifty-one per cent of the animals (N=105) engaged in R/R 1-9 times per day; 12% (N=25) would do R/R on 10 or more occasions per day; 5% (N=10) would do R/R, but not on a daily basis; and a further 32% (N=66) were never seen to engage in R/R at all.

Gould and Bres (1986) published results of another survey, concerning 117 gorillas housed in 17 zoos. The authors do not state the geographical location of these surveyed zoos, but were themselves based at a North American zoo. They found that 81/117 gorillas (69%) would regurgitate and reingest their food, although they do not report how often, but it is clear that this was (and may still be) a common behaviour in zoo-housed Gorillas. Baker and Easley (1996, p.404) also report that R/R is “not a rare behaviour” in Chimpanzees, citing a conference paper by Brent (1992) showing that 18/32 (56%) of singly-caged laboratory Chimpanzees engaged in it. More recently, Birkett and Newton-Fisher (2011) reported that R/R occurred in 30% (N=12) of the zoo-housed Chimpanzees across all six research groups in their UK- and US-based zoo study of 40 Chimpanzees.

When considering gorillas of different ages, the Gould & Bres (1986) survey showed that only 19% (N=5/26) of gorillas aged under 5 years old would do R/R. Consequently, the authors argue that a more accurate representation of the prevalence of R/R can be gained by considering only those animals aged over 5 years, which increases the frequency of R/R in their study to 84% of the gorilla population (N=76/91 Gorillas). That said, the median age of onset of R/R in their study population of Gorillas was younger, at 3 years old (range 2-6.5 years; N=9 gorillas).

Similarly, a recent survey on N=154 Orangutans in the Association of Zoos and Aquariums Species Survival Plan® (SSP) population in North American zoos, found that the youngest Orangutans to engage in R/R were 5 years old (Cassella *et al.*, 2012). In that study, the overall prevalence of R/R was 32% (N=49 out of 154 animals), which rose to 36% (N=60) after removing the 17 Orangutans aged 4 years or younger from the analysis. More information on the age of onset of R/R in individuals would be useful in future studies, although historic data are likely to be lacking in most cases, as the information may simply have not have been recorded at the time (Hill & Broom, 2009; Fidgett *et al*., 2013). Zoo records are often not useful (currently) for retrospective behavioural research, but this can improve with more goal-driven, systematic collection of behavioural data in the future (Hosey *et al*., 2012).

The survey results by Gould and Bres (1986) showed that R/R was reportedly less common in 'captive-born and mother-reared' Gorillas, than in 'captive-born and hand-reared' individuals, or those who were wild-caught, but they found no sex differences. Conversely, Cassella *et al.* (2012) found a trend towards a sex difference in R/R in Orangutans (N=137), which approached statistical significance, with more females (42%) than males (26%) engaging in R/R. They did find a significant species bias, with Sumatran Orangutans having the lowest prevalence of R/R (18%), compared to Bornean and hybrid Orangutans at 45% and 42%, respectively, although possible reasons for this are not offered (Cassella *et al.*, 2012).

The results of the Cassella *et al.* (2012) survey, and the Birkett and Newton-Fisher (2011) study, show an encouragingly lower overall prevalence of R/R in Orangutans (36%) and Chimpanzees (30%), respectively, than the authors of earlier work on Gorillas had found (e.g. Akers & Schildkraut, 1985; Gould & Bres, 1986). This might reflect improvements to the housing and husbandry of great apes in captivity since the earlier surveys were conducted, as has been the general trend in modern zoo animal care, and/or it might reflect a species difference in this behaviour (e.g. Cassella *et al.*, 2012). Nevertheless, it still represents a considerable number of animals, and warrants further investigation.

There is a lack of quantifiable data on current rates of R/R in most zoo-housed great apes on a regional basis and/or worldwide. The current literature search also did not reveal any reports of R/R occurring in wild-born great apes housed in African or South East Asian sanctuaries (i.e. rescue/rehabilitation centres), and so it would be useful for this to be investigated further. It may be that R/R is absent from those populations of apes, in which case useful lessons for zoos may be learnt from the sanctuaries. Conversely, it may be the case that R/R does occur in wild-born sanctuary apes, but has simply not been reported to date. If the latter is true, useful insights into this behaviour, and how to eliminate or prevent it, may be gained by zoos and sanctuaries working together as part of a 'One Plan' approach (Barongi *et al.*, 2015).

R/R AS A POTENTIALLY INJURIOUS BEHAVIOUR

Given what is known about the clinical consequences of 'rumination' in people, the behavioural repertoires of great apes in the wild (who are not known to do R/R), and that in many countries there is a legal, not to mention ethical, obligation to meet the biological needs of zoo animals, including needs for good welfare (e.g. Hosey *et al.*, 2013), it is the author's opinion, and those of others researching this behaviour, that we should be concerned about R/R as an abnormal behaviour (e.g. see Pizzutto *et* al., 2007; Struck *et al*., 2007; Hill, 2009).

There are no known published reports of physical consequences of oral acid in gorillas or other non-human apes as a consequence of doing R/R, as is seen in people. This could mean that non-human apes can cope with the acid better than people can, or that it has simply not been investigated systematically yet, but the available evidence suggests it is potentially injurious in Western lowland gorillas (Hill, 2009). In that study, 11 samples of regurgitant were collected non-invasively and opportunistically from Gorillas at a British zoo, whose veterinarian reported no other known health problems in those individuals. The pH of the regurgitant was then compared to the pH samples of the food that was ingested originally. Results showed that the regurgitated food samples were significantly more acidic than the original food, indicating that stomach acid was also being regurgitated into the mouth, as in human 'ruminators'.

Some anecdotal reports suggest health problems in Gorillas that do R/R, which may be linked to this behaviour. These include sores in the kinds of areas where the regurgitant has come into contact with the animal's skin repeatedly (e.g. back of hand, sides of mouth); and/or ulceration at the back of the throat (Anon., pers. comm.), or underweight animals with poor body condition that cannot otherwise be explained (Anon., pers. comm.; pers. obs). This is an area that should be investigated further, so that firmer conclusions can be drawn about any possible consequences to the physical health of the animals that do R/R. In reality, this type of investigation is more likely to be opportunistic, as (fortunately) mortality rates in zoo-housed apes are low in modern zoos and, depending on region of the world, it is often not possible (legally and/or ethically) to perform invasive research studies on zoo-housed animals; see Hill (2009), Hill & Broom (2009) and Hill & Smith (2013) for further discussion on this.

As well as considering any potential consequences there may be to the physical health of animals that engage in R/R, it is also necessary to understand the reasons why animals might be doing R/R in the first place. This may assist zoos in reducing or eliminating R/R where it does already occur, and help prevent the behaviour developing in additional individuals in the future (Hill & Broom, 2009).

FACTORS THAT MAY AFFECT R/R

One of the challenges with investigating the factors that affect R/R in great apes is that, to date, only relatively small-scale studies have been undertaken to try to reduce or eliminate the behaviour from animals' repertoires, and so findings cannot necessarily be generalised to the wider population. Furthermore, the behaviour appears to be multifactorial (Cooper & Hull, 2017), and also varies by individual animal (Miller & Tobey, 2012). This issue is not uncommon in scientific assessments of welfare, as welfare is about how an individual animal attempts to cope with its environment, and each individual should be considered in its own right (Hill & Broom, 2009; Hosey *et al*., 2013).

In the following sub-sections, I give an overview of some of the findings from the published literature, indicating the range of factors that might be involved in R/R. As a note of caution, the factors are not necessarily mutually exclusive, and further investigation may reveal considerable overlap and interaction with each other, before we can identify causal factors confidently. Thus, there is no known "one treatment cures all" option for R/R currently.

Feeding-related factors (including nutrition and opportunities to feed)

Most of the research on R/R to date has focused on Gorillas, and has found a range of feeding-related factors to be involved. When captive Gorillas regurgitate food, it is often in association with feeding times, and especially the post-prandial period (e.g. Lukas *et al.*, 1999), which suggests that zoos should consider increasing the availability (but not necessarily quantity) of food provided throughout the day, as food is ubiquitously available in the wild. To avoid unnecessary duplication here, the reader is also directed to the review of earlier work by Lukas (1999), focusing on nutritional and motivational factors that might contribute to R/R in zoo-housed Gorillas, for additional information on potential feeding-related factors. Many of the studies reviewed by Lukas (1999) involve very small sample sizes, because of the nature of much of the zoo-based welfare research (Hill & Broom, 2009). Thus, they are important as case studies, but further research is needed to test how applicable the findings are to the wider population of great apes in zoos. The main factors reviewed by Lukas (1999) tend to suggest that provision of browse and removal of fruit from the diet reduces (but doesn't eliminate) R/R in Gorillas, but the author does not show whether this apparent effect is caused by nutritional or occupational factors ('continuous-feeding hypothesis'). It is also important to test this for other great apes in consideration of their biological needs as well.

'Continuous feeding hypothesis', and possible gustatory factors

Masi et al. (2009) found that a group of wild Western lowland gorillas at Bai Hokou, Central African Republic, spent most of its time feeding (about 67%), which is similar to findings by Sabater Pi (1993) for wild Gorillas at Rio Muni, Equatorial Guinea (about 72% of their time feeding and foraging). Similarly, wild Chimpanzees are known to spend 30-60% of their daily activity budgets engaged in feeding and foraging (e.g. Struck *et al*., 2007). It is unlikely that most zoos around the world are replicating this in the time budgets of their great apes currently, and a focus on targeted enrichment efforts relating to the complexity of the feeding environment, coupled with a species-appropriate diet, should be considered as part of the strategy for reducing (if not eliminating) R/R in great apes. Lukas *et al*. (1999) found that the reingestion component of the R/R cycle in Gorillas is the most time-consuming, with 77% of the cycle devoted to it, as opposed to only 17% for pre-regurgitation behaviours, and actual regurgitation only taking up 5% of the cycle. This further

suggests the role of R/R (or specifically reingestion) in prolonging an animal's opportunities to feed, in the absence of other, more biologically-appropriate, options in zoos.

Struck *et al.* (2007) and Fuller *et al*. (2017) have emphasised that differences between the activity budgets of wild and captive Chimpanzees and Gorillas, respectively, can be put down to feeding behaviours. Along with other research on zoo Gorillas (and possibly other great ape species), this suggests that occupational factors to do with food may be involved in some individuals. For example, the virtual elimination of R/R (and hair plucking) has been reported for a silverback Gorilla at a German zoo, following an increase in opportunities for continuous feeding, in the absence of actual dietary changes (Hill, 2004). This finding shows that occupational factors were contributing to R/R, at least for that individual. It is important to consider animal welfare at the individual level, as different animals will respond to their environment in different ways (Hill & Broom, 2009). For example. Rooney and Sleeman (1998) analysed their Gorilla R/R data at a group level, and not by individual, but found no significant difference in R/R as a consequence of their manipulable and feeding-related enrichment efforts. Whilst this could be a genuine case of unsuccessful enrichment efforts for those individuals, it is also possible that a different conclusion may have been reached if the animals had been analysed as individuals.

Gould & Bres (1986) showed that feeding browse to a male and female gorilla at a US zoo can increase the time spent feeding, presumably because it is a naturally fibrous type of food and takes longer to eat than softer food, such as fruit, again prolonging the feeding opportunities. The provision of browse in that study also led to a reduction in time spent in R/R, from 45·8% to 11·2% for the female, and from 11·5 to 5·7% for the male. Fuller *et al.,* (2017) also investigated the role of browse in R/R, by manipulating the amount of forage material given to three male Gorillas at a US zoo. Their results showed that when forage material was provided daily for two weeks, none of the gorillas were observed doing R/R; two of the males only engaged in R/R when no additional forage material was provided, with individual differences shown in the size of response. Furthermore, their results showed a significant increase in time spent doing normal feeding-related behaviours, and that these became more similar to wild time budgets. Thus, their study confirms foraging materials, such as browse, to be an important resource for the three captive gorillas in this study (and, based on the natural history of Western lowland gorillas, possibly the species as a whole).

A further study on R/R in another two captive gorillas in a US zoo also shows a reduction in this behaviour in response to dietary manipulations (Wiard, 1992). One gorilla received hay, browse and novelty food items, including cereal, frozen ice treats and peanut butter in cardboard tubes. The other gorilla received a variety of foods, including hay and browse, but food was presented more evenly across the day. In both cases these dietary manipulations were made in addition to their regular, more complex diet. Wiard (1992) argues that the reduction in R/R in her two subjects

resulted from a combination of an increase in time spent foraging, and the novelty of the enrichment effort. R/R by one of the gorillas increased slightly several months after the efforts commenced, although not to original levels, and so it is clear that R/R and efficacy of husbandry changes should continue to be monitored in the long term, in case there is a loss of effect, and techniques can be readjusted as required. The Gorillas in the Hill (2004) study were monitored by their keepers after the formal study had finished, and the reduction and virtual elimination of R/R in the silverback remained in the long-term, so the novelty did not seem to have worn off for that individual.

Struck *et al*. (2007) have examined the effects of providing increased foraging material to a single male Chimpanzee at a research and housing facility in the USA, housed with four other males in a stable social group. This male had been a known regurgitator for 7 years, and previous attempts to reduce his R/R by replacing fruit with high fibre vegetables in his diet had been unsuccessful. He had responded previously to pharmacological treatment with a selective serotonin reuptake inhibitor (SSRI), whereby his R/R has been reduced, but not eliminated. SSRIs are also used in people, in the treatment of conditions such as anxiety (American Psychiatric Association, 2013). The Struck *et al*. (2007) case study showed that increased opportunities resulted in an increase in time spent foraging and feeding from 4.9% in the baseline to over 28% during the forage condition (including unsweetened cereal, sunflower seeds, peanuts, popcorn, and chicken scratch), and over 48% in the browse treatment (palm (*Washingtonia robusta*) fronds and stems, bamboo (*Phyllostachys* spp), Palo Verde (*Cercidium microphyllum*), and Ash (*Fraxinus anomala*) branches). However, R/R increased during the forage condition, from around 2% (baseline) to around 4%, but was virtually eliminated in the browse condition, dropping from just over 2% of time in the baseline to 0.3% in the treatment phase. The authors argue that the reduction in R/R following inclusion of browse in the diet was likely to be due to increased satiation from the greater fibre content provided by the browse. The increase in R/R during the forage phase was unpredicted by the authors, but the forage materials they used were consumed quickly and, therefore, may not have resulted in a feeling of satiation. Another possible explanation could relate to the continuous-feeding hypothesis, whereby the quickly-consumed forage resulted in excessive ‘free’ time. This could be understimulating and lead to boredom and/or frustration, as the animal did not have continuous access to food. A different selection of forage items and ways of presenting them could potentially yield different results if they require longer to find, process and consume (e.g. Hill, 2004).

In a different phase of the Gould & Bres (1986) study, the authors showed that R/R increased in three known regurgitators when their meals were experimentally blended and served as a more easily-digestible liquid. The blended diet led to a doubling of feeding rate in the four gorillas to whom it was served (the fourth Gorilla was not a regurgitator). The blended-meal consumption time

reduced to 12-20 minutes, compared to their normal 30-60 minute baseline, with onset of R/R occurring quickly, 14 seconds to 12 minutes after consumption.

Liquids *per se* in the diet do not necessarily seem to be the issue, but possibly the texture or flavour (or at least for some Gorillas). A study of 19 zoo-housed Gorillas at a US zoo found that removing milk from the diet and replacing it with an equal volume of undiluted fruit juice resulted in a reduction of R/R by 28% (Lukas *et al.*, 1999). The authors argue that this reduction could have been the result of the texture of milk making it easy to regurgitate, or that milk was a favoured food item that the animals perhaps wanted more of when they regurgitated it. Hediger (1964, p. 132 describes R/R as the '… fictitious increase in the quantity of food …' and argues that it prolongs, or repeats, '… the feeling of pleasure connected with feeding … through vomiting [sic] and eating again'. Some regurgitating Gorillas do make food calls ('singing') that sound similar to those that occur when gorillas are anticipating a meal or are eating favoured food, such as mangoes and other sweet fruit (pers. obs). A Gorilla may also supplant the regurgitator, thus enabling the supplanting individual to eat the regurgitant, suggesting that the taste is not unpleasant (Lukas *et al.*, 1999). The same has been observed in Chimpanzees (Baker & Easley, 1996), a Marmoset (J. Keeley, pers. comm.) and people with rumination disorder.

When food is available too readily, or meal times are spaced out too widely as they might be for some zoo animals, opportunities to engage in food-seeking and food-obtaining activities are thus limited. This is likely to be frustrating to the animals concerned, because they are unable to fulfil a need (Broom & Johnson, 2000) and because it probably results in hunger. R/R could be the only means by which these animals can increase their opportunities to feed, by eating the same food items several times over. A silverback gorilla in an under-stimulating environment has been observed unsuccessfully attempting to regurgitate food after an already-prolonged period of R/R (Hill, 2004). Presumably, because the gastric contents were too small in volume to regurgitate at that moment, he would then do coprophagy, and subsequently regurgitate and reingest his faeces. Whilst this was an extreme case, R/R of faeces may be the only option for a gorilla that is hungry, has a need to carry out feeding-related activities and has already regurgitated his stomach contents to an extreme, in the absence of a normal way to express this need.

Nutritional qualities of food

While sample sizes in R/R studies of apes are often small and husbandry practices may have changed a lot in the elapsed time since the earlier studies, it seems that for at least some individuals, R/R can be done because of a feeding environment that is inappropriate to their needs. Thanks to further research on the natural feeding ecology of free-living great apes, we have better knowledge and understanding that fruit should not constitute such a large part of the captive diet for some great apes as has traditionally been the case, and readers are respectfully reminded to

consult their most-up-to-date regional zoo association husbandry guidelines regularly, as well as their institution's veterinarian/nutritionist, regarding current best practice advice (e.g. for AZA Chimpanzees: AZA Ape TAG (2010); for EAZA Gorillas: Abelló *et al*., 2017), before making any dietary changes, and should ensure that any positive or negative effects on the animals are monitored and dealt with.

Cassella *et al.* (2012) studied four Bornean orangutans *Pongo pygmaeus* under the normal husbandry routines of that zoo, to examine any relationship between R/R and feeding schedules. They found that time spent feeding was generally low, but peaked when food was provided first thing and increased again when an afternoon snack was provided. They also found that R/R seemed to be linked to feeding times, but that R/R was reduced when browse was available, and that provision of browse almost tripled the amount of time spent feeding. Three of the four study animals were regurgitators, and two of these showed a significant increase in R/R after sweet foods. Albeit using small numbers of animals, this study may provide further evidence that zoos should be providing a browse-rich diet for certain species of great apes, and should be cautious of providing sweet foods, such as commercially-available fruit. This may not be appropriate for animals such as Bonobos or Chimpanzees (Miller & Tobey, 2012), due to being primarily frugivorous, depending on the nutritional quality (and thus biological appropriateness) of the zoo diets.

Less *et al*. (2014a and 2014b) monitored behaviour and health of Gorillas in their US study during a low-starch dietary change in which commercial biscuits (not commonly used in European zoos) were removed, and fruit was reduced and replaced with more fibrous option (e.g. leafy greens, vegetables and alfalfa hay). Significant improvements in behaviour, including R/R, were reported following the change (Less *et al*., 2014a), as well as reductions in insulin and serum cholesterol levels (Less *et al*., 2014b). In making any dietary change, caregivers should exercise caution and consider a slow reduction/increase or removal/addition of the items from the diet, to avoid any adverse physical or behavioural effects of changing the diet. If some biologically-inappropriate dietary items are to be removed/reduced, but are 'preferred' by some individuals (e.g. because of the sweetness), it should be remembered that not all preferences are beneficial to the animal (Broom & Johnson, 2000). Thus, I would argue that caregivers should not feel 'bullied' by the animals into giving them inappropriate food items just because they like to eat them; more biologically-suitable enrichment should be provided instead (notwithstanding the occasional 'treat', where appropriate).

As Cabana *et al.* (2017) highlight, nutritional composition of wild fruits is different to those commercially available to zoos, with the latter typically having been cultivated for increased palatability and sweetness. Consequently, zoo fruit tends to have a higher sugar and energy

content, but is lower in fibre, minerals and vitamins. In addition to links to R/R, diet is associated with conditions such as obesity, cardiovascular disease, diabetes and dental problems, amongst others (e.g. Plowman, 2013; Cabana *et al.*, 2017). However, the evidence to date suggests that individual animals may have different reasons for doing R/R and there are sometimes unpredicted results. For example, Lukas *et al.* (2011) found that browse led to an increase in R/R two make gorillas at a US zoo, which was not expected. Thus, it is important that zoos adopt an evidence-based approach and ensure they monitor and document the effects of any husbandry changes carefully at the individual level, including changes to diet, especially in case of any unpredicted results.

Temporal / seasonal factors

The Akers and Schildkraut (1985) study of a male and female gorilla at zoos in the USA revealed a pattern of a late afternoon peak in R/R across the various study conditions, following the last feed of the day, representing a large inter-meal interval. The authors argue that R/R may have been a compensatory behaviour, to extend the feeding opportunities enforced by captivity; if so, this would fit in with the continuous-feeding hypothesis referred to earlier. Lukas *et al*. (1999) observed a similar pattern in their study of zoo-housed Gorillas, as R/R would increase when animals were given a drink of milk during their evening meal. The authors also noted an apparent seasonal effect of R/R, with gorillas engaging in more R/R in the winter, when they were more active, than in the summer, when the weather was hotter and animals were less active. This should be investigated in future studies, as it may be that husbandry should also vary with the seasons when managing R/R.

Social factors

An emerging area to investigate further in future studies is the possibility that R/R might be related to social behaviour in some individuals. Gould & Bres (1986) found that social deficits during early development may contribute to the occurrence of R/R in later life, but their sample size for captive-born, mother-reared animals, was low, making realistic comparisons with hand-reared animals more problematic. As hand-rearing great apes is now less common, this might not be so relevant to modern zoos, but might be to sanctuaries dealing with rescued orphaned apes, who have experienced significant early-life trauma. Some human infants with rumination disorder are known to regurgitate as a consequence of a 'failed interaction' with caregiver (which is not necessarily to place the blame on the caregiver) (e.g. Malcolm *et al*., 1997; Wagaman *et al*., 1998; Thame *et al*., 2000), and so a 'social hypothesis' may fit for (some) non-human great apes as well.

Baker and Easley (1996) found no relationship between R/R and social disturbance in their Chimpanzee study; similarly, Herrelko *et al*., (2015) found no change in R/R during the merging and introduction of two chimpanzee groups. In contrast, Miller & Tobey (2012) investigated R/R in 14 Bonobos housed at two zoos undergoing management changes in their group social structure.

They found that the amount of time that Bonobos spent doing R/R differed from week to week, as would be expected because of behavioural plasticity, as animals have the ability to change their behaviour in response to environmental changes (e.g. Mery & Burns, 2010). However, Miller & Tobey (2012) found a significant positive correlation between the percentage of time Bonobos spent doing R/R and aggressive behaviours at one of their study sites, and a significant negative correlation between R/R and affiliative behaviours at the other study site. While the results differ, they indicate some sort of a relationship between R/R and social behaviour in those individuals. Additional research is needed in this area to see if it is possible to determine a causal effect, or if some other underlying stressor is contributing to the increase in both R/R and aggression. Furthermore, the definition of R/R used by Miller & Tobey (2012) includes what appears to be hand-assisted vomiting, rather than 'true' (i.e. effortless, non-vomit) regurgitation, as defined in other works (e.g. see Lukas, 1999; Hill, 2009; Fuller *et al*., 2017), and so it would be useful to re-examine this for these two types of behaviour.

Another possibility is that some individual great apes are learning to do R/R by observing and copying other members in their group. Opportunities for social learning and cultural transmission in zoo-housed great apes, within the context of normal feeding, has been reported (e.g. Gustafsson *et al*., 2014). Whilst the possibility of R/R being socially enhanced or learned has yet to be investigated systematically, Lukas *et al*. (1999) observed infant and juvenile Gorillas watching adults while they carried out R/R, and we know from other studies that first onset of R/R seems to occur around the age of 5 years (e.g. Gould & Bres, 1986), which may fit with this.

Medical factors

The current literature search found no published studies investigating a (non-psychological) medical cause of R/R in great apes, but that is not to say such a cause might not be found in at least some individuals in the future. In most cases it has probably not been investigated thoroughly in great apes, though the male Chimpanzee in the R/R study by Struck *et al.* (2007) would routinely undergo biannual physical examinations, dental evaluations, and haematology and serum chemistry analyses, the results of which suggested he was otherwise in good physical condition. However, better diagnostic approaches could perhaps be employed to rule out other medical causes of R/R type behaviour that may currently be being overlooked. For example, eight laboratory-housed Baboons *Papio hamadryas* were used as a model for GORD in people (Glover *et al.*, 2008). Six of these animals showed clinical signs that included regurgitation (as opposed to vomiting). Two of the study animals were diagnosed with spontaneous GORD following endoscopic examination and biopsy, whereas the remaining six were diagnosed with GORD under post-mortem examination. Glover *et al.* (2008) argue that GORD may serve as an alternative explanation for regurgitation in some non-human primates. If a causal link is found in at least some individuals, it opens the door for a pharmacological treatment method, such as antacids, in addition

to appropriate husbandry and housing. In the Glover *et al*., (2008) study, it may have been the case that the regurgitating animals did R/R in addition to having GORD, but this is not known.

Even if GORD is found to be a cause of R/R is some zoo-housed great apes, there is strong evidence that stress not only can cause, but also increase the severity of, problems associated with the gastrointestinal tract. This is also the case in Pigs *Sus scrofa scrofa* that have significantly more oesophagogastric lesions when housed in 'standard' (barren) environments compared with enriched housing (Ramis *et al.*, 2005). No oesophagogastric ulcers were observed in animals in the enriched housing (N=203), compared with 17% of the 200 pigs in the standard housing (Ramis *et al.*, 2005). It is also widely regarded that there is a connection between diet and GORD in people, such as a larger meal size promoting acid reflux, and it is also believed that certain types of food, such as those that are more acidic, also promote it. If the same is true for non-human apes, this could have implications for the provision of food in zoos and sanctuaries, both in terms of the nutritional content and the way food is presented (see previous section). Thus, zoos and sanctuaries should continue to develop species-appropriate, goal-driven environmental enrichment efforts to assist in their provision of optimal care for animals, with a wide range of benefits.

One of the arguments that Glover *et al.* (2008) make regarding R/R or GORD, is that studies of R/R in non-human primates have been unable to demonstrate a long-term improvement in this behaviour in a large number of individuals and hence, they argue, GORD could be the cause. Whilst this might (or might not) be found to be the case, the truth is there have simply not been enough studies of R/R in zoo animals to date, and so our understanding of this behaviour across the great ape species is still very limited. As considered by Hill & Broom (2009), there are methodological challenges associated with obtaining physiological data that might be relevant to investigations of R/R in great apes, but the potential for such studies should be explored if these can meet (and ideally exceed) ethical and legal requirements.

Other factors

An important aspect to consider might be individual personality and its potential role in R/R. Personality research is a growing sub-discipline in animal welfare science, and it may be useful if future research can combine investigations of individuals' personality and R/R (and other abnormal behaviours). For example, Robinson *et al*. (2017) state that work is underway in this field to validate animal welfare and personality questionnaires, and it is likely that these kinds of studies will increase in the future. This will add to our understanding of behaviours like R/R and other aspects of animal welfare (Schaefer & Steklis (2014), and thus aid our ability to manage captive apes more optimally. Sample sizes in R/R studies conducted thus far are too small to draw conclusions about the role of individual factors. It is important to study behaviours like R/R at the level of the individual, as this is what animal welfare is about (Hill & Broom, 2009; Stoinski *et al*.,

2012) and, the more studies that are carried out, the greater our knowledge will be about R/R as a means of attempting to cope with some aspect(s) of the captive environment, and what zoos can do to improve this. Possible effects of age and sex on R/R have been considered in a previous section.

Herrelko *et al*., (2015) studied the impact of changes in available space and enclosure areas during the merging and introduction of two chimpanzee groups (N=11 ex-laboratory/safari park chimpanzees; N=11 zoo chimpanzees), housed at a British zoo. Whilst some significant changes in behaviour were observed when more enclosure areas were available, rates of R/R (only done by the ex/laboratory/safari park group) remained unchanged. Likewise, R/R did not change in response to total size of available space, or across different phases of the introduction to the other group, indicating that these factors were not contributing to R/R in those individuals at that time, but other individuals might potentially respond differently to these in future studies.

FUTURE DIRECTIONS

There are still many gaps in our knowledge and understanding of R/R, which need addressing in future research if we are to provide the best possible care for these animals. There appear to be several possible, and not necessarily mutually-exclusive, motivational reasons for doing R/R and different animals within the same group can behave in different ways, in addition to the possibility that GORD is a cause in at least some individual animals. Regardless of the cause(s) of R/R, it is not part of the normal feeding mechanism in great apes and has never been reported to occur in free-living, wild members of the species, and thus it is classified as an abnormal behaviour (e.g. Pizzutto *et al.*, 2007; Hill, 2009). If it is indeed shown to be sometimes caused by GORD (Glover *et al.*, 2008), or some as yet undetermined other medical problem, or an animal's feeding or social environment, or something else altogether, it still represents a welfare issue that zoos should address. Depending on what further investigation reveals to us, this might be achieved via pharmacological means and/or changes in animal husbandry and housing or other aspects of captive care.

One of the risks with R/R being observed often (Lukas, 1999) is that it could be seen by some animal care staff as 'normal', or at least as 'not abnormal' (Zeller, 1991). By 'normalizing' this behaviour, we risk overlooking important implications for animal welfare, and any secondary effects of this behaviour on the conservation actions of zoos. This might have implications for the preservation of normal, diverse behavioural repertoires in zoo and sanctuary animals (Hill & Broom, 2009), and any future reintroduction efforts should these be feasible (IUCN/SSC, 2013). It might also impact negatively on visitor satisfaction and empathy for the state of these animals in the wild, thus affecting zoos' attempts to increase their commitment to conservation (Barongi *et al.*, 2015).

Consequently, it is important that zoos should continue to be involved in further research to investigate R/R. This will enable us to take steps to reduce the likelihood that any more individual great apes will start doing this behaviour in the first place, as well to try to reduce or eliminate it from individuals that already do it. In this way, zoos and sanctuaries can continue to develop, evaluate and share best practice techniques for the care of great apes. Zoos that do not have the capacity to develop and carry out their own research programmes should engage with their regional (e.g. SSP / EEP) coordinators, and with academic colleagues in universities (Reid *et al*., 2008), to co-develop behavioural and physiological projects that will help to fill in the many gaps in our knowledge relating to R/R. Multi-zoo studies are ideal in terms of larger sample sizes (Hill & Broom, 2009), but are not without their challenges as additional variables are then introduced (Hosey, 1997).

It is beyond the scope of this review paper to go into detail about specific methods for future studies into R/R, but several methodological texts might be useful to the reader (e.g. on measuring behaviour scientifically: Martin & Bateson, 2007; Stamp Dawkins, 2007; assessments of welfare: Hill & Broom, 2009; zoo-based research: Bishop *et al*., 2013). It is clear from the work reviewed in the current paper that some main research areas could be of use to our knowledge and management of R/R in all zoo-housed great ape species, including (but not restricted to):

1. Current prevalence of R/R in great apes for the global captive population (a study by the author is in preparation to address this).
2. Behavioural studies (on any topic) reporting R/R as a behavioural category, at the level of individual animals (and also reporting non-occurrence of R/R in individuals that do not do it, including all age categories). These should also include documentation of any idiosyncratic, repetitive pre- or post-regurgitate behaviours (part of establishing an evidence base for patterns or sequences in R/R).
3. Non-invasive studies (at the individual level) of behaviour and health, testing the potential causal factors or links involved in R/R, such as those relating to diet; food presentation; animal personality; social environment; etc.
4. Veterinary investigations to rule out medical causes of R/R.
5. Comparative studies between zoo and wild-born sanctuary apes, who do not seem to do R/R (e.g. diet; behavioural opportunities; interactions with human care-givers; development of the behaviour (if it is eventually found to occur in sanctuary apes)).
6. Knowledge-sharing with those working on similar problems in people, e.g. rumination disorder and GORD, including causes and treatment, as more is known about these conditions in people.

7. Physiological investigations of R/R in great apes, to examine any evidence of physical consequences of the oral acid. These could be done *post mortem*, and/or during other medical investigations (if done ethically and without compromising the animals' welfare further (e.g. due to invasive procedures)).
8. The impact of R/R, and other abnormal behaviours, on zoo visitor satisfaction, as it is arguably an unpleasant behaviour to observe (Lukas *et al*., 1999). For example, Godinez *et al*. (2013) found that zoo visitors' dwell times at a US zoo were longer at the Jaguar (*Panthera onca*) enclosure, and their 'visit satisfaction' ratings were higher, when animals were observed doing normal active behaviours, as opposed to stereotypies or being out of sight. If R/R in great apes is affecting visitor satisfaction and dwell times in the same way, it may hinder zoos' efforts to engage the public with conservation action for these species (Barongi et al., 2015), in addition to the welfare concerns.

ACKNOWLEDGEMENTS

The author wishes to thank Don Broom for earlier discussions on this topic; Frank Reitkerk, Zjef Pereboom and Fiona Fiskin for their invitation to write this paper, and two anonymous reviewers for their helpful comments.

REFERENCES

Abelló, Mª. T., Rietkerk, F. & Bemment, N. (Eds.) (2017): *EAZA Great Ape Taxon Advisory Group: Best Practice Guidelines for Gorillas (*Gorilla gorilla gorilla). Amsterdam: EAZA Executive Office. Retrieved from: https://www.eaza.net/assets/Uploads/CCC/2017-BPG-Gorilla-approved.pdf.

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

American Psychiatric Association (2013): *Diagnostic and statistical manual of mental disorders* (5th edn). Arlington, VA: American Psychiatric Association.

Arbuckle, K. (2013): Folklore husbandry and a philosophical model for the design of captive management regimes. *Herpetological Review* **44:** 448–452.

AZA Ape TAG (2010): *Chimpanzee* (Pan troglodytes) *Care Manual*. Silver Spring, MD: Association of Zoos and Aquariums. Retrieved from: https://www.aza.org/animal-care-manuals.

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

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

Barongi, R., Fisken, F. A., Parker, M. & Gusset, M. (Eds) (2015): *Committing to conservation: the world zoo and aquarium conservation strategy.* Gland, Switzerland: WAZA Executive Office.

Birkett, L.P. & Newton-Fisher, N. E. (2011): How abnormal is the behaviour of captive, zoo-living chimpanzees? PLoS ONE **6**(6): e20101. DOI:10.1371/journal.pone.0020101.

Bishop, J., Hosey, G. & Plowman, A. (Eds.) (2013): *Handbook of Zoo Research, Guidelines for Conducting Research in Zoos*. London. BIAZA. Retrieved from: https://biaza.org.uk/downloader/583.

Broom, D. M. & Johnson, K. G. (2000): *Stress and animal welfare*. Dordrecht: Kluwer Academic Publishers.

Cabana, F., Jasmi, R. & Maguire, R. (2017): Great ape nutrition: low-sugar and high-fibre diets can lead to increased natural behaviours, decreased regurgitation and reingestion, and reversal of prediabetes. *International Zoo Yearbook* **52.** DOI:10.1111/izy.12172.

Cassella, C. M., Mills, A. & Lukas, K. E. (2012): Prevalence of regurgitation and reingestion in orangutans housed in North American zoos and an examination of factors influencing its occurrence in a single group of Bornean orangutans. *Zoo Biology* **31:** 609–620.

Cooper, J. E. & Hull, G. (2017): *Gorilla pathology and health, with a catalogue of preserved materials*. London: Academic Press.

Fidgett, A.L., Pullen, P. K., Brunger, D., Warren, A., Collins, C., Farmer, H., Elliot, J., Beeston, D. & Showell, Z. (2013): Introduction to research using zoo records. In: J. Bishop, G. Hosey & A. Plowman (Eds.), *Handbook of Zoo Research: Guidelines for Conducting Research in Zoos* (pp. 80-94). London: BIAZA. Retrieved from https://biaza.org.uk/downloader/583.

Fuller, G., Murray, A., Thueme, M., McGuire, M., Vonk, J. & Allard, S. (2017): Behavioral and hormonal responses to the availability of forage material in Western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology* **37.** DOI: 10.1002/zoo.21393.

Glover, E. J., Leland, M. M., Dick Jr, E. J. & Hubbard, G. B. (2008): Gastroesophageal reflux disease in baboons (*Papio* sp.): a new animal model. *Journal of Medical Primatolology* **37:** 18–25.

Godinez, A. M., Fernandez, E. J. & Morrissey, K. (2013): Visitor behaviors and perceptions of jaguar activities. *Anthrozoös* **26:** 613–619.

Gould, E. & Bres, M. (1986): Regurgitation in gorillas: possible model for human eating disorders (rumination/bulimia). *Journal of Developmental and Behavioral Pediatrics* **7:** 314–319.

Gustafsson, E., Saint Jalme, M., Bomsel, M-C. & Krief, S. (2014): Food neophobia and social learning opportunities in great apes. International Journal of Primatology **35**:1037–1071.

Hediger, H. (1964): *Wild animals in captivity*. New York: Dover Publications.

Herrelko, E. S., Buchanan-Smith, H. M. & Vick, S. J. (2015): Perception of available space during chimpanzee introductions: Number of accessible areas is more important than enclosure size. *Zoo Biology* **34:** 397-405.

Hill, S. P. (2004): *Behavioural and physiological investigations of welfare in captive western lowland gorillas (*Gorilla gorilla gorilla*).* PhD thesis, University of Cambridge, UK.

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

Hill, S. P. & Broom, D. M. (2009): Measuring zoo animal welfare: theory and practice. *Zoo Biology* **28:** 531–544.

Hill, S. P. & Smith, T. (2013): Monitoring adrenal response in zoo animals as an indicator of welfare. In: J. Bishop, G. Hosey & A. Plowman (Eds.), *Handbook of Zoo Research: Guidelines for Conducting Research in Zoos* (pp. 95-107). London: BIAZA. Retrieved from https://biaza.org.uk/downloader/583.

Hopper, L. M., Freeman, H. D. & Ross, S. R. (2016): Reconsidering coprophagy as an indicator of negative welfare for captive chimpanzees. *Applied Animal Behaviour Science* **176:** 112–119.

Hosey, G. R. (1997): Behavioural research in zoos: Academic perspectives. *Applied Animal Behaviour Science* **51**: 199-207.

Hosey, G., Hill, S. P. & Lherbier, M. L. (2012): Can zoo records help answer behavioral research questions? The case of the left-handed lemurs (*Lemur catta*). *Zoo Biology* **31**: 189–196.

Hosey, G., Melfi, V. & Pankhurst, S. (2013): *Zoo Animals: Behaviour, management and welfare*. Oxford: Oxford University Press.

IUCN/SSC (2013): *Guidelines for reintroductions and other conservation translocations:* version 1.0. Gland, Switzerland: IUCN Species Survival Commission.

Landis, B. & Lambroza, A. (2001): A respiratory biofeedback solution for the rumination syndrome. *Biological Psychology* **56:** 79-80.

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

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

Lukas, K. E. (1999): A review of the 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. & 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.

Lukas, K. E., Less, E. H. & Dennis, P. M. (2011): A pilot study on the effects of dietary resistant starch on serum cholesterol and regurgitation and reingestion in zoo gorillas. In *Proceedings of the XXIII congress of the International Primatological Society, Kyoto University, Kyoto, Japan,*

September 12–17, 2010: 715. Kyoto: Kyoto University for International Primatological Society. Available at http://primate-society.com/ips/public/ips_program/IPS10-715.pdf

Malcolm, A., Thumshirn, M. B., Camilleri, M. & Williams, D. E. (1997): Rumination syndrome. *Mayo Clinic Proceedings* **72:** 646–652.

Maple, T. L. (2014): Elevating the priority of zoo animal welfare: the chief executive as an agent of reform. *Zoo Biology* **33:** 1–7.

Martin, P. and Bateson, P. (2007): *Measuring Behaviour: An Introductory Guide*. Cambridge: Cambridge University Press.

Masi, S., Cipolletta, C. & Robbins, M. M. (2009): Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. *American Journal of Primatology* **71:** 91–100.

Melfi, V. A. (2009): There are big gaps in our knowledge, and thus approach, to zoo animal welfare: a case for evidence-based zoo animal management. *Zoo Biology* **28:** 574–588.

Mery, F. & Burns, J. G. (2010): Behavioural plasticity: an interaction between evolution and experience. *Evolutionary Ecology* **24:** 571–583.

Miller, L. J. & Tobey, J. R. (2012): Regurgitation and reingestion in bonobos (*Pan paniscus*): relationships between abnormal and social behaviour. *Applied Animal Behaviour Science* **141**(1–2): 65–70.

Monagas, J., Ritwik, P., Kolomensky, A., Acosta, J., Kay, D., Clendaniel, L. & Hyman, P. E. (2017): Rumination syndrome and dental erosions in children. *Journal of Pediatric Gastroenterology and Nutrition* **64:** 930–932.

Pizzutto, C. S., Nichi, M., Ramiro Corrêa, S. H., Ades, C. & De Barros Vaz Guimarães, M. A. (2007): Reduction of abnormal behavior in a gorilla (*Gorilla gorilla gorilla*) through social interaction with human beings. *Laboratory Primate Newsletter* **46:** 3-6.

Pizzutto, C.S, Sgai, M.G.F.G., Lopes, D.A., Pessutti, C., Nunes, A., Furtado, P.V., de Oliveira, C.A. & Marcelo A.B.V. Guimarães, M.A.B.V. (2015): Relation between the level of self-mutilation and the concentration of fecal metabolites of glucocorticoids in captive chimpanzees (*Pan troglodytes*). *Pesquisa Veterinaria Brasileira* **35**(1): 62-66.

Plowman, A. (2013): Diet review and change for monkeys at Paignton Zoo Environmental Park. *Journal of Zoo and Aquarium Research* **1**(2): 73–78.

Ramis, G., Gomez, S., Pallares, F. J. & Munoz, A. (2005): Comparison of the severity of esophagogastric, lung and limb lesions at slaughter in pigs reared under standard and enriched conditions. *Animal Welfare* **14:** 27–34.

Reid, G. McG., Macdonald, A. A., Fidgett, A. L., Hiddinga, B. & Leus, K. (2008): Developing the research potential of zoos and aquaria: The EAZA Research Strategy. Amsterdam: EAZA Executive Office. Retrieved from https://www.eaza.net/assets/Uploads/Strategies/EAZA-Research-Strategy-2008.pdf.

Robinson, L. M., Altschul, D. M., Wallace, E. K., Úbeda, Y., Llorente, M., Machanda, Z. Slocombe, K. E., Leach, M. C., Waran, N. K. & Weiss, A. (2017):Chimpanzees with positive welfare are happier, extraverted, and emotionally stable*. Applied Animal Behaviour Science* **191:** 90–97.

Rojahn, J., Barnard-Brak, L., Medeiros, K. and Schroeder, S.R. (2016): Stereotyped behaviours as precursors of self-injurious behaviours: a longitudinal study with infants and toddlers at risk for developmental delay. *Journal of Intellectual Disability Research* **60:** 156–166.

Rooney, M. B. & Sleeman, J. (1998): Effects of selected behavioral enrichment devices on behavior of western lowland gorillas (*Gorilla gorilla gorilla*). *Journal of Applied Animal Welfare Science* **1**(4): 339-351.

Rose, P. E., Croft, D. P. & Lee, R. (2014): A review of captive flamingo (Phoenicopteridae) welfare: A synthesis of current knowledge and future directions. *International Zoo Yearbook* **48:** 139-155.

Sabater Pi, J. (1993): *Gorilas y Chimpancés del África Occidental: Estudio Comparativo de su Conducta y Ecología en Libertad* [*Gorillas and chimpanzees of western Africa: comparative studies of their behaviour and ecology in the wild*]. México: Fondo de Cultura Económica.

Schaefer, S. A. & Steklis, H. D. (2014): Personality and subjective well-being in captive male western lowland gorillas living in bachelor groups. *American Journal of Primatology* **76**:879–889.

Stamp Dawkins, M. (2007): *Observing animal behaviour: Design and analysis of quantitative data*. Oxford: Oxford University Press.

Stoinski, T. S., Jaicks, H. F. & Drayton, L. A. (2012): Visitor effects on the behavior of captive western lowland gorillas: The importance of individual differences in examining welfare. *Zoo Biology* **31**(5), 586-599.

Strombeck, D. R. (1979): *Small animal gastroenterology*. Davis, CA: Stonegate Publishing.

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. *Lab Animal* **36**(1): 35-38. DOI:10.1038/laban0107-35.

Thame, M. M., Burton, K. A. & Forrester, T. E. (2000): The human ruminant. *West Indian Medical Journal* **49:** 172–174.

Wagaman, J. R., Williams, D. E. & Camilleri, M. (1998): Behavioral intervention for the treatment of rumination. *Journal of Pediatric Gastroenterology and Nutrition* **27:** 596–598.

Wiard, J. (1992): Regurgitation and reingestion (R&R) in lowland gorillas at the Oklahoma City Zoo. *Gorilla Gazette* **6:** 6–7.

Zeller, A. C. (1991): Human response to primate deviance. *Anthropologica* **33:** 39–68.