The Welfare of Zoo-housed Chimpanzees (Pan troglodytes) with Special Attention to Auditory Enrichment

Emma Katherine Wallace

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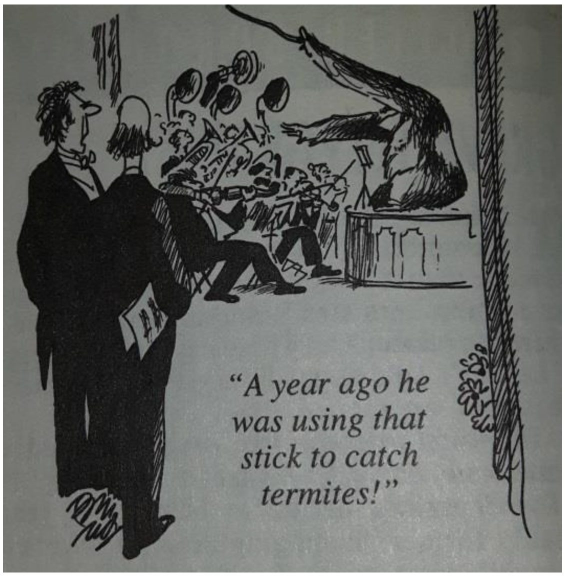
Abstract

Modern zoos house millions of wild animals but also aim to conduct animal research, educate visitors about the natural world and support conservation programmes via funding and encouraging wildlife-friendly actions by the public. However, the benefit to conservation efforts and species living in the wild, through fundraising and increasing public awareness, may come at the cost of the animals living within zoos. In this thesis I focussed on the welfare of zoo-housed chimpanzees due to their endangered status and public popularity. I investigated potential social, dietary and visitor related triggers for anxiety-related behaviours (yawning and scratching) and regurgitation and reingestion (R/R). Despite interesting trends, no immediate triggers for these behaviours were found. However, long-term data showed the frequency with which individuals engage in R/R reduced over time when part of a complex group inhabiting an enclosure encouraging natural behaviours and social dynamics. I also examined if music, frequently broadcast to captive chimpanzees, provides any enriching effect on their welfare. Both observational and experimental research suggested that whilst music does not appear to have any obvious positive welfare effects it is equally not detrimental. The final study explored whether public education, one of assumed benefits associated with having animals in zoos, is achieved via 'Keeper Talks'. They were effective at demonstrating to adult visitors that touchscreens are an effective form of enrichment for chimpanzees but the talks had no significant effect on their knowledge of other issues covered, or any area of knowledge in young people. Further investigation showed that zoo professionals have inaccurate estimates of visitor knowledge and that assessment methods do not always align with educational goals. Overall, the findings in this thesis highlight the importance of research within zoos, which can lead to a better understanding of barriers to good animal welfare, utilisation of only positive welfare interventions and maximisation of educational potential.

Table of Contents

List of Tables

List of Figures



This thesis is dedicated to three primates whom I loved:

Roger Smith

A gentle, grumpy Silverback

23rd June 1946 to 5th March 2013

Herbert Whittle

A magical, dancing Sifaka

7th May 1916 to 14th June 2013

Pearl

Pat Butcher in Chimpanzee form, who was never without a carrot

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Author's Declaration

This thesis contains original work that was carried out by the author, Emma Katherine Wallace, under the supervision of Dr Katie Slocombe. Each of the studies presented, with the exception of study 1 in chapter 5, was conducted in accordance with the ethical standards of the University of York and was approved by the Department of Biology Ethics Committee or the Department of Psychology Ethics Committee as well as Edinburgh Zoo. The work in this thesis has not been submitted for examination at this or any other institution for another award. All sources are acknowledged as References.

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Chapter 3: I collected and coded the data along with Karoline Körfer and Benjamin Benti . I analysed all data. Katie Slocombe and Bridget Waller aided with the design of the study and provided intellectual input throughout. Katie Slocombe contributed to manuscript edits.
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Chapter 1 – Modern Zoo Principles

History of Zoos and Captive Animals

Whilst private collections of animals or menageries have existed for thousands of years, the first zoo opened in 1752 in Vienna. It was not until 1779 that members of the public were allowed access. The earliest zoos initially had numerous deaths in the animal collections, which led to the enclosures being made more hygienic by introducing 'hard architecture' where enclosures were primarily made of concrete and metal for ease of cleaning (Young, 2003). The use of such unnatural, aseptic enclosures, coupled with the animals usually being housed singly, led to the expression of stereotypic behaviours, defined as "repetitive, unchanging behaviours with no obvious goals or functions" (Cheyne, 2006). However, it was not until the 1930s that the first observations of such behaviour were recorded (Meyer-Holzapfel, 1968) and even later that the first measures were taken to counteract them. It is important to try to tackle the problem of stereotypic behaviours and poor welfare (for full definition see Chapter Two) in zoos as it not only maximises the psychological wellbeing of the animals, but also increases the education value of zoo exhibits (Carlstead, 1998; Ironmonger et al., 1992).

Modern Zoos

Modern accredited zoos now reflect the contemporary roles of zoos; conservation, education and research (Kreger et al., 1998). In 1986, Soule et al. introduced the concept of zoos as an 'Ark' to protect species from extinction through captive breeding programmes, which is known as ex situ conservation. Not only are zoos able to breed species to ensure their survival but they have also been fundamental in the endurance of wild populations of animals, referred to as in situ conservation. For instance, the Smithsonian National Zoological Park Golden Lion Tamarin Conservation Program was founded in 1983 with the aim of saving the 'Critically Endangered' Golden Lion tamarins (*Leontopithecus rosalia*). The program involved conservation projects in Brazil's Atlantic forest fragments, captive breeding and relocations of captive zoo-born individuals into the wild. In the year 2000, the number of individuals living in groups started by captive born animals was 359 (Kierulff *et al.* 2002a, b). In 2003 the IUCN downgraded the species to 'Endangered' (www.iucnredlist.org/details/11506/0) and by 2005 the total estimate of all golden lion tamarins, including those originating from captivity, was 1500 (Holst et al., 2006).

The research conducted within zoos was a key part in the golden lion tamarin success. Little was known about the species before 1972 when the Smithsonian National Zoological Park began research into how best to care for them in captivity as well as their reproduction and behaviour (Kleiman and Mallinson, 1998). The application of this knowledge has led to an increase in numbers of tamarins in captivity. In 1973 there were fewer than 70 animals in 20 different zoos but by the end of 1995 143 institutions housed 485 individuals (Ballou and Sherr, 1997).

Research conducted in the wild also benefits husbandry standards for animals in captive settings. Slow lorises (*Nycticebus* ssp.) are kept in 40 different zoos in Europe but they do not appear to breed well in captivity and many individuals suffer from illnesses such as kidney disease and obesity (Fitch- Snyder et al., 2001). These problems are believed to be due to their captive diet (Fuller et al. 2014), which can include dairy products, animal protein and fruit (Fitch- Snyder et al., 2001). In recent years, research from the wild has shown that the species eats exudates (plant gum or sap) and insects (Streicher , 2009), highlighting the inadequacy of captive diets. Changes to the diet of a male slow loris at Painton Zoo, that included the elimination of animal protein and fruit, led to significant improvements in rates of feeding and travelling behaviours, generally thought to be indicators of improved welfare, whilst rates of abnormal behaviours were significantly lower (Cabana and Plowman, 2014). Another example of wild based research aiding captive animals is an electronic tool that has been created to compare the movements and behaviours of captive groups of chimpanzees with previous observations of wild individuals (Thorpe et al., 2016). The tool is then able to make suggested modifications to the design of the current enclosure to create more wild-type behaviours.

For zoos to obtain funds for conservation and research projects, fee-paying visitors are needed. It is estimated that over 700 million people, or 10% of the world's population, visit zoos each year (Therkelsen and Lottrup, 2015). In addition to gaining funding that can be directly applied toward conservation initiatives, public zoos provide an opportunity to educate the broader public about these issues, as well as topics such as animal biology and behaviour. If zoos are able to capitalise on educating these visitors on issues like species extinction, conservation initiatives they can undertake at home, such as choosing products containing sustainable palm oil, and the importance of animal welfare this could have global impacts on the conservation movement. Zoos can use a variety of techniques for educating their visitors, which I shall discuss over the coming paragraphs. More specifically, I will explore how enclosure design can maximise the education opportunities for visitors (Hosey, 2005), and discuss frequently used interpretive signage, sessions for school children with designated educators and informative talks.

Landscape Immersive was first used by Jones et al. (1976) to refer to an enclosure, or an entire zoo, that is designed to look like the animal's natural habitat whilst allowing the space to be shared by both the animals and visitors. Housing a species in an immersive enclosure can help the public to 'place' the animal in its natural environment. This type of enclosure has been found to change the behaviour of visitors, making them quieter around and more respectful to the animals (Hutchinson et al., 1978) as well as increasing the time visitors spent at an enclosure (Johnston, 1998). Visitors even believe that the animal welfare is better in immersive enclosures (Melfi, McCormick and Gibbs, 2004).

Interpretive signage used for educational purposes can be highly cost effective as signs are generally only changed once every few years and can be used to impart information to the public about the animals within each enclosure. However, a study by Ross and Gilliespie (2009) found that only 9% of visitors interacted with signage in a brand new mixed species enclosure. This suggests that even in facilities where the signage is up to date and does not look faded, a very small number of visitors are actually looking at the information and knowledge retention is likely to have been even lower, although this has not yet been tested. 'Hands on' or interactive signage has been shown to increase interaction in zoo visitors (Lukas and Ross, 2005), which has led to many zoos adopting this type of signage as they can be effective at delivering an educational message (Bowler, Buchanan-Smith and Whiten, 2012; Whitehouse et al., 2015; Derwin and Piper, 1988; Andersen, 2003).

Many zoos have specialist education departments that employ zoo educators to work with visiting school groups by running lessons and activities within the zoo setting. These sessions can allow children to gain hands-on experiences through handling items (Patrick and Tunnicliffe, 2013), such as bones and fur, and/or animals whilst learning about their biology, ecology and conservation issues (Andersen, 2003). Some of the primary benefits of these sessions include fostering affection for animals and science more generally (Sanford, 2014), consolidating information learnt at school (Sanford, 2014) and introducing zoo-based careers that students may not have considered previously (Doolittle and Grand, 1995).

A common method of bringing educational messages to the wider zoo-visiting public is using talks or public displays. Many studies have demonstrated the benefits of this medium for disseminating information. A study of visitors who observed Sea Otters (*Enhydra lutris*) at Monterey Bay Aquarium enjoyed the experience more at times when a member of staff was present (Mortan, 2001). Dwell time of visitors viewing a Clouded Leopard (*Neofelis nebulosa*) exhibit increased from 55 seconds to 185 seconds when presentations were delivered (Povey and Rios, 2002). It was also found that the visitors present during the presentations had a greater likelihood of using signage or asking questions (Povey and Rios, 2002). Having an active element in the talk, such as feeding or training the animals, has been found to increase the publics' attention (Anderson et al., 2003; Perdue, Stoinski & Maple, 2012) and can also increase their ability to remember key messages. For example, a study by Heinrich and Birney (1992) surveyed adults at Brookfield Zoo's Children's Zoo after watching the "Animal All-Stars Show" and by telephone six weeks later. Up to 83% of the participants were able to remember the educational messages put across during the show after six weeks.

The above studies demonstrate that zoos have the potential to educate the public on many issues relating to wildlife and can be used to justify the existence of animals within zoos for educational purposes. However, whilst there are thousands of accredited zoos worldwide, published assessments of educational impact by individual institutions are very rare and more research is needed in this area (Balmford et al., 2007; RSPCA, 2006).

Conclusion

The roles of zoos have changed dramatically in the past 150 years. They now aim to be centres where conservation, research and education interact to promote the future health and welfare of both captive and wild animals. In the next chapter I shall explore the topic of zoo animal welfare in more depth as well as identifying methods of improving the welfare of these animals.

Chapter 2 – The Welfare of Chimpanzees in Captivity

The welfare of captive animals is of importance not only to maximise the psychological wellbeing of the animals, but also to improve the quality and validity of research conducted in captive settings, and to maximise education opportunities in zoos (Hosey, 2005). Before measures can be taken to improve the quality of life of a captive animal the concept of animal welfare, as well as how it is currently measured, needs to be understood.

What is Animal Welfare?

Welfare is a notoriously difficult term to define and many ideas exist about how to do so (Young, 2003), but one of the most commonly used definitions is how an animal functions biologically in its environment, how well an animal maintains homeostasis (copes) and how it 'feels' (Duncan and Fraser, 1997). In common parlance, the term 'stress' has negative associations and as such it is assumed that if an animal is 'stressed' this is a bad thing. However, it is important to remember that animals in the wild experience high levels of stress as well as those in captivity (Hosey, 2005). The evolution of the acute stress response served to enable animals to escape danger, and the activation of this response is considered by some to be something that can be a beneficial part of long-term husbandry (Chamove and Moodie, 1990; Moodie and Chamove, 1990). As such, infrequent bouts of acute stress should not necessarily be considered a welfare issue.

Measuring Welfare

As previously mentioned, defining the term welfare is considered a difficult task but to measure it is thought of as even more difficult (Mason and Mendl, 1993). Observing animal behaviour is one of the most frequently used methods of measuring welfare. Displaying a wide range of behaviours, the ability to express strongly preferred behaviours, behavioural indicators of pleasure and displaying species-typical behaviours (Swaisgood, 2007; Broom, 1999) are regularly used to identify animals experiencing good welfare and behavioural deviations from the species norm are commonly used to identify those suffering from poor welfare. I shall now focus on how increases in rates of aggression, abnormal behaviours, allogrooming and play can be used to assess captive animal welfare.

Aggression is a natural behaviour that is displayed to some extent by almost all species of animals in the wild. However, if this behaviour is not managed it can be problematic in captivity as limited enclosure space means that animals cannot always escape their aggressors and can result in wounding. In humans, activation of the stress response has been shown to greatly contribute to aggressive behaviour. When female humans are given additional cortisol (a hormone produced during the stress response) they behave more aggressively (Böhnke et al., 2010). Increasing cortisol levels in rats also increases aggressive behaviour (Kruk et al., 2004). This relationship between aggression and the stress response suggests that high levels of aggression can be an indicator of poor welfare.

Abnormal behaviours, unlike aggression, are categorised as a set of behaviours that are performed either solely in captivity or at a much higher level than in the wild. These behaviours include coprophagy, drinking urine, hair plucking and regurgitation and reingestion (Birkett and Newton-Fisher, 2011) and can be considered indicators of underlying mental health issues or suffering (Birkett and Newton-Fisher, 2011). If an individual animal performs the same set of behaviours, often in a repetitive manner, this is considered a stereotypie (Cheyne, 2006). Sterotypies are more frequently found in captive animals compared to their wild counterparts, suggesting that these behaviours are a result of captivity. They are frequently used as a measure of negative welfare as they often develop due to sub-optimal environments or psychologically challenging events (Mason, 1991a). In non-human primates, self-directed behaviours, such as yawning, scratching, body shaking and self-grooming, are short term indicators of anxiety. If an animal displays any of these behaviours it suggests that they are attempting to cope with an aversive stimulus (Higham et al., 2009). Long-term expression of anxiety behaviours can suggest the animal is experiencing poor welfare.

As well as using behavioural observations to indicate poor welfare, it is also important to look for the presence of positive behaviours, such as allogrooming (Boissy et al., 2007). Allogrooming is defined as one individual moving the hair or fur of another individual and removing ectoparasites from them (Fa and Southwick, 1988). Being involved in grooming, whether as the actor or receipient, has been shown to reduce stress levels (Schino and Aurelli, 2008) and the presence of grooming is said to be an indicator of good or even very good welfare, when viewed on a scale from very good to very poor (Broom, 1991).

Another behaviour that Boissy et al. (2007) identified as an indicator of positive emotions in captive animals is play. It is a behaviour that can be difficult to distinguish from other behaviours, but Burghart (2005) suggested that play can be identified as behaviours that do not directly contribute to current fitness, that are self-rewarding, differ from the adult version of the behaviours, happen repeatedly but not in a stereotypical manner and are initiated whilst there are no threats to the animal. Play can be considered a luxury behaviour (Held and Spinka, 2011) as the behaviour disappears during times of hardship. For example, food shortages during the process of weaning have been found to supress play in domestic piglets (Donaldson et al., 2002) and rates of play in the free-ranging rhesus macaques in Cayo Santigo reduced by 17 times during a 22 day period of acute food shortage (Loy, 1970). However, whilst play seems an excellent behaviour for identifying positive welfare it can sometimes occur during periods of stress (Held and Spika, 2011) making it difficult to ascertain if the performance of the behaviour due to good or poor welfare. Also, bouts of play may even end in true aggression in some species (Blackshaw et al., 1997) so care should be taken when interpreting the behaviour but it is, on balance, an indicator of positive welfare.

A negative aspect of using behavioural observations to assess welfare can be the length of time required for thorough evaluations. To avoid this, subjective measures of animal welfare are now being used more commonly within the scientific community as they can be conducted more quickly by relying on existing human-animal relationships. A study by Weiss et al. (2011) looked at the wellbeing of 184 zoo-housed orang-utans (*Pongo pygmaeus*) using seven points scales on the frequency of positive against negative moods, pleasure gained from social interactions, ability to attain goals and human (caretaker) perceived 'happiness' of the animal. The results of these measures were then compared with data on longevity and it was found that individuals that were rated as being 'happy' lived longer. There are, however, many issues with this approach. The scales used to measure the animals' welfare were originally used for humans but adapted for use with orangutans. Some of the questions were inherently anthropocentric, including asking how happy the rater would be as that orangutan. A veterinary review of animal quality of life assessments (QOL) (Yeates and Main, 2009) argued that anthropocentric measures, such as happiness, should not be used for assessing QOL. They state that it requires humans to 'read the minds' of the animals in question, which can lead to differences in interpretation between different people (Graham et al., 2002).

The use of physiological measures of welfare, such as faecal/urinary cortisol and heart rate, is thought to avoid the issues faced with subjective measures. They are becoming more commonly used due to the fact that they are non-invasive and do not necessarily require an individual to spend time observing the behaviour of the animals but the combination of direct behavioural observations and physiological data is optimum. For example, Boinski et al. (1999) found that giving brown capuchins access to enrichment devices lead to decreases in abnormal behaviour as well as decreases in both plasma and faecal cortisol levels. However, it is worth noting that it can be difficult to establish if physiological changes are related to changes in welfare. Cortisol levels are known to fluctuate throughout the day (Ladewig, 1984) even when there is no stressor present and rises in cortisol levels can occur when an animal eats or copulates (Toates, 1995). With heart rate, increases can indicate fear in animals but equally a reduction in heart rate, especially if coupled with freezing behaviour, can also show an animal is fearful (Mason and Mendl, 1993). An additional problem with physiological measures is that the equipment and facilities required to process samples can be prohibitively costly and may require extensive training to be able to use it correctly.

Challenges to welfare in a zoo environment

The combination of factors that make zoos different from other types of captive environments can lead to welfare problems for a wide variety of animal species. The zoo environment is very different for captive animals from that which they would experience in the wild and is also different from other captive conditions, such as research facilities. What makes zoos a unique form of environment is the combination of regular exposure to unfamiliar visitors, often in high numbers, restricted space and animal care routines (e.g. feeds; restricting access to certain enclosure areas for cleaning)(Hosey, 2005).

Challenges to welfare of zoo-housed Chimpanzees

I have chosen to specifically focus on the welfare of zoo-housed chimpanzees due to the fact that chimpanzees are currently classified as endangered, meaning that captive bred individuals may be required to contribute to wild populations in the future (Hvilsom et al., 2013). For this reason, it is especially important that any pure-bred chimpanzee should experience good welfare to encourage the expression of species typical behaviours and avoid the development of abnormal behaviours. As chimpanzees are considered to be a very intelligent species (Inoue and Matsuzawa, 2007; Inoue-Nakamura and Matsuzawa, 1997) that display a wide variety of complex behaviours (Whiten et al., 1999; Stokes and Byrne, 2001), zoos face many challenges to provide them with good welfare. Another reason for choosing chimpanzees as a study species is that they are one of the most closely related species to human beings (The Chimpanzee Sequencing & Analysis Consortium, 2005) and are commonly seen in the media, from natural history documentaries to advertisements. If it is possible to increase public awareness of the importance of improving captive welfare using chimpanzees, a species that is very familiar to zoo-visitors, it is hoped that this will lead to a change in attitude towards the welfare of all zoo animals.

Zoo-housed chimpanzees are managed by humans in many ways that can be detrimental to them experiencing good welfare. Over the course of the next few paragraphs I shall examine how enclosure size, social group size and composition, the movement of individuals between groups, hand-raising infants and restricting breeding of specific individuals can negatively affect chimpanzee welfare.

In the wild, chimpanzees travel large distances each day, often spending much time foraging for and consuming food. The size of chimpanzees home ranges varies from 7 to 10 km^2 at the fertile forests of Gombe and Budongo (Goodall, 1986; Newton-Fisher, 2003) to estimates of 50 km^2 in the Senegalese sights of Mt. Assirik and Fongoli, and Semliki in Uganda where the habitat is much drier (Baldwin et al., 1982). In captivity, enclosure sizes are much smaller than even the smallest chimpanzee territories. In addition, food, which is usually high in energy compared to wild foods (Plowman et al., 2013), is provided by keepers, often at set times of the day. This combination of factors drastically reduces the amount of time spent travelling compared to wild counterparts and increases the chances of obesity and other health related issue. The time that wild chimpanzees spend travelling, is free for captive animals and this often leads to a lack of opportunities to express species-specific behaviour, referred to as boredom (Wemelsfelder, 1993). Animals need to occupy their time by doing something and in the absence of anything in their environment that allows them to perform any other behaviours, stereotypies may occur in an attempt to cope (Wemelsfelder, 1993).

It is very difficult for zoos to provide chimpanzees with a social group that is natural in size, composition or fission-fusion dymanics. The size of communities of chimpanzees in the wild varies between 10 and 150 (Watts, 2002), which are much larger than those in captivity and often those few individuals are forced to spend all of their time together. Wild communities of chimpanzees split into sub-groups or sub-parties each day, the formation of which is constantly changing. This is known as fission-fusion dynamics (Kummer, 1971). This social system is incredibly difficult to facilitate within zoos unless enclosures are specifically designed with this in mind, creating many separate areas so the animals can split into more natural temporary sub-groups.

To maintain genetically diverse breeding populations, individuals are either frequently moved between captive groups or are not moved from their natal group once they have reached sexual maturation, which can lead to inbreeding. Inbreeding is a problem for both wild and zoo animals as it can reduce rates of offspring survival (Ralls and Ballou, 1983). In the wild inbreeding is avoided by the majority of females emigrating from their natal group once they reach sexual maturity (Stumpf, 2007) and those who remain in their natal group decreasing the time spent associating with maternal siblings (Pusey, 1980).In captivity, if measures are taken to avoid inbreeding, as females can reach sexual maturity earlier than in the wild (Coe et al., 1979), individuals can be moved at from their natal group before they are ready to do so. Some zoos will also aim to keep the number of adult males within a group at a low level in an attempt to reduce rates of aggression. Moving males from their natal group, which does not occur in the wild, can break up strong male-male bonds that exist in chimpanzees (Gilby and Wrangham, 2008), that confer several important benefits, including support to reach higher positions of dominance (Nishida and Hosaka, 1996).

In some instances when mother may naturally reject her offspring the decision may be made to hand raise the infant. The practice of raising chimpanzee infants without a mother has been shown to produce individuals that may not display species typical behaviours and avoid social interaction (Turner et al., 1969), have higher incidences of rocking and self-sucking behaviours (Nash et al., 1999) and show less advanced cognitive and emotional development (Van Ijzendoorn et al., 2008). This leads to the introduction of less socially adept individuals into socially complex groups, which may negatively affect group dynamics. Additionally, female chimpanzees may be unable to care for their offspring if they themselves never learnt how to from their mother or others in their natal community (Porton and Niebruegge, 2006).

Equally, international breeding programmes promote the reproduction of non-hybrid individuals, so not all adult chimpanzees are allowed to breed. This can dramatically affect the social bonds and behavioural repertoires of the infants within these groups. Having fewer infants present at any time may result in infants having fewer individuals to interact with through play. As play is believed to be a vital behaviour for the development of bodily control and learning to cope with unexpected situations (Spinka et al., 2001), having a reduced number of play partners may hinder infant development. Longitudinal research is needed to ascertain if the social behaviour and cognitive abilities of mother-reared, group-housed infant chimpanzees that developed as a lone infant are different from those who grew up with other infants in the group.

Measures of Poor Welfare in Chimpanzees

I have just highlighted several potential causes of poor welfare for zoo-housed chimpanzees. There are numerous behaviours displayed by these animals than can be used to identify if they are experiencing poor welfare.

As outlined above, whilst aggression is part of chimpanzees' natural behavioural repertoire (Muller and Wrangham, 2004; Mitani et al., 2010), increases in rates of aggression in captivity, especially events that lead to wounding, can be an indicator of poor welfare. Abnormal behaviours, such as hair plucking and drinking urine, may be frequently observed in captive chimpanzees. A study by Birkett and Newton-Fisher (2011) looked at the behaviours of 40 chimpanzees living in six different accredited zoos. They found that all of the 40 individuals showed at least two abnormal behaviours and identified a total of 37 different forms of abnormal and self-injurious behaviours.

Regurgitation and reingestion (R/R) is a behaviour that has been observed in captive chimpanzees (Baker and Easley, 1996) as well as bonobos (Miller and Tobey, 2012), gorillas (Akers and Schildkraut, 1985) and lion-tailed macaques (Mallapur et al., 2005). It is thought to indicate previous stress or current distress. The behaviour is defined as the voluntary movement of food from the stomach or the oesophagus into the hand, the mouth or on to a substrate followed by the consumption of the regurgitant (Gould and Bres, 1986a). It is a behaviour that can lead to serious health issues, such as oesophageal strictures, ulcers, reflux, oesophagitis, intestinal obstruction, oesophageal motor disorders and pulmonary aspiration (Wyngaarden et al., 1992). Whilst there are many proposed triggers for the behaviour, such as boredom (Baker, 2004; 1997) or diet consumed (Morgan et al., 1993), no one universal cause of the behaviour in captive chimpanzees has been identified.

How do we improve welfare in zoos?

The most commonly used method for improving the welfare of captive animals is environmental enrichment. Enrichment is defined as "an animal husbandry principle that seeks to enhance the quality of captive animal care by providing the environmental stimuli necessary for optimal psychological or physiological well-being" (Shepherdson, 1998).

There are two separate approaches to creating enrichment; behavioural engineering and naturalistic enrichment (Young, 2003).Behavioural engineering addresses a ‘behavioural need’ by the use of an unnatural device, which leads to the expression of natural behaviour, such as the use of wires to animate a dead rabbit to encourage cheetahs to hunt (Williams et al., 1996). The main problem with the use of behavioural engineering devices is that they do not necessarily encourage natural behaviours (Hutchins et al., 1978a; 1984). They may instead promote behaviours that ensure the animal stays in good physical condition that would not be observed in the wild (e.g. meat attached to the top of tall pole via a bungee cord that big cats have to pull down; this is not a specific hunting behaviour for big cats but strengthens muscles that may otherwise be unused during their day to day lives) or meet a behavioural need, such as meerkats ‘digging’ through small, plastic balls to find food rather than digging through sand as they would in the wild. Problems also arise when trying to educate the public as seeing non-naturalistic devices can send confusing messages to visitors (Kreger et al., 1998).

Naturalistic enrichment emerged as an alternative to behavioural engineering. The design of enclosures and the enrichment used within them was aimed to be as close to nature as possible to promote species-typical behaviours seen in the wild (Hancocks, 1980; Forthman-Quick, 1984; Maple and Finlay, 1989). The assumption, however, that the expression, or lack of it, by captive animals of behaviours observed in their wild counterparts is a sign of good or poor welfare respectively may not hold true. Veasey et al. (1996b) argue that, rather than the more widely held belief that allowing animals to express wild-type behaviours causes to them experiencing good welfare, the expression of such behaviours is merely correlated with good welfare and, as such, if an animal is unable to express wild-type behaviours they are not necessarily experiencing poor welfare.. This would mean that it is not vital for captive animals to engage in wild-type behaviours and, therefore, ensuring captive environments are as naturalistic as possible may not be as important as some, including zoo visitors, believe it to be.

Some zoos have preferences for natural forms of enrichment due to the public demonstrating a preference for natural-looking animal enclosures (Seidensticker and Doherty, 1996). However, the provision of either natural or behavioural engineering forms of enrichment can lead to positive welfare changes for captive animals, providing that the type of enrichment selected meets a behavioural need for the intended species. There are five different types of environmental enrichment, as identified and named by Bloomsmith et al., (1991), which I shall describe in detail below:

Social Enrichment

Social Enrichment relates to the use of physical, visual or auditory contact with other individuals of social species. As the majority of accredited zoos provide social groupings for many of their animals, social enrichment is most frequently used in research facilities where animals are housed singly and social contact can be provided artificially. Many animal species live in social groups in the wild in order to avoid predation and to improve the likelihood of finding food (Dunbar, 1988). Social living also provides complex mental stimulation, which is unlikely to be reproduced by any enrichment device (Humphrey, 1976), making social contact incredibly important for captive animals. For example, black tufted-ear marmosets (*Callithrix kuhlii*) were isolated from their pair mate then played their mate's vocalisations, those of an unknown individual or no calls. Individuals that were isolated had higher physiological stress levels than those that remained with their pair mates. These higher levels were significantly reduced upon hearing the calls from their pair mate but not those from the stranger (Rukstalis and French, 2005). However, social living alone is not believed to be enough to ensure good welfare as animals, especially primates, additionally require complex social and physical environments, cognitive challenges or control over aspects of their environment (Buchanan-Smith, 2011).

Occupational or Cognitive Enrichment

One of the key problems animals face in captivity is a lack of control over their environment (Markowitz, 1982). Providing animals with psychological puzzles or devices that allow animals control over their environment can, therefore, improve welfare. It is suggested that animals that have even a small degree of choice or control over their environment are less stressed and better able to cope with stressors. When rhesus macaques (*Macaca mulatta*) had control over high intensity noise, cortisol levels were the same as if there was no noise. Losing control was found to have the same effect as never having control, the exception being that losing it created more aggression, possibly out of frustration, where as those monkeys that had never had control showed less social contact (Hanson et al., 1976). Additionally, captive animals consistently prefer to work for their food even when the same food is available without having to undertake any work to obtain it. This is a phenomenon known as contrafreeloading (see Inglis et al., 1997 for review of the literature). This desire to work for food can be combined with cognitive puzzles to enrich animals and using such puzzles may even lead to reductions in abnormal behaviours (Clark, 2011). An opaque tube maze, referred to as a cognitive challenge device (CCD), was used with six zoo-housed chimpanzees (Clark and Smith, 2013). The animals had either food or tokens that had to be guided through the maze to a point where they could be easily extracted. Whilst interaction with the device was generally low, only 2.5% of the total observation time, time spent engaging in social play significantly increased at times when the device was present in the enclosure and scratching (an indicator of anxiety) significantly decreased when the individuals interacted with the device.

Physical Enrichment

Structures and toys in enclosures can allow the expression of species-specific behaviours. For example, gerbils displaying stereotypic digging behaviour showed no improvement when given sand in which to dig. However, when they were given dens with imitation tunnels, like those they create in the wild, this prevented the stereotypical digging from developing (Wiedenmayer, 1997).

Nutritional Enrichment

Nutritional enrichment is the provision of a variety of food items and methods of presentation to the animals. In the wild, some primate species can spend up to 45% of their day foraging or engaging in food related behaviour (gorillas – Harcourt, 1987). In zoos, food is usually provided at certain times of the day and little effort is required on the part of the primate in order to obtain it. Providing nutritional enrichment can alleviate this issue. For example, giving browse (freshly cut tree branches) to orang-utans at Chester zoo increased the amount of time the individuals spent foraging and reduced their inactivity (Birke, 2002).

Sensory Enrichment

This uses visual, olfactory and auditory stimulus to enrich the lives of the animals. Sensory enrichment works best when the sense that is being stimulated is one that an animal relies on most heavily (Wells, 2009). An analysis of published articles on enrichment was undertaken (de Azevedo et al., 2007) and found that sensory enrichment has the lowest success rate of the different types; 65% compared to 80% for physical enrichment. This is most likely due to differences in perception of sensory stimuli between humans and other animals, for example, the ultrasound from a television in 'stand-by' mode can barely be heard by humans but can kill a chipmunk housed in the same room within two days (Meredith, 2002). Also, sensory stimuli are made up of many different aspects. For example, a piece of music consists of frequency, tempo and tone. It could be any one, or a combination of several, of these aspects that has a positive, or negative, effect.

Chimpanzees and Enrichment

Environmental enrichment can be very effective at improving the welfare of captive chimpanzees (Schapiro et al., 1993; Brent and Belik, 1997) and is frequently used in zoos (Wells, 2009; Clark and Smith, 2013). However, finding appropriate forms of enrichment can be very difficult because of the complexity of their social systems and intelligence (Vick et al., 2000). Additionally, durability can be important if the enrichment item is to be used multiple times (Brent and Stone, 1998) due to the strength and manual dexterity of chimpanzees (Finch, 1943; Corp and Byrne, 2002) . Chimpanzees also have a preference for novel objects and habituation to an object can happen quickly (Bloomsmith et al., 1990) meaning that different devices should be rotated (Wallace, 1988) or new ideas for enrichment should be generated constantly.

When designing a new form of enrichment for chimpanzees it is important to think of what aspect(s) of their lives require enriching and which type of enrichment will do so most effectively (Buchanan-Smith, 2011). Additionally, when a novel form of enrichment is provided for any species it is vital that its impact is assessed. One method of assessing the success of a form of enrichment is how much the target animals use it. However, a recent study of macaws has suggested that even low interaction with an enrichment device can lead to significant positive behavioural changes (Reimer et al., 2016).

I believe that a more appropriate method for assessing enrichment is, therefore, to investigate behaviour changes associated with the provision of the enrichment. For something to be classed as enriching for an animal it must be seen to have a positive effect on animal welfare by reducing negative or abnormal behaviours and increasing positive forms of activity. As mentioned previously, levels of aggression in captive chimpanzees should be monitored closely and, therefore, enrichment should not cause levels of aggression to increase. If, however, reductions in aggression and abnormal behaviours that are commonly observed in chimpanzees (Birkett and Newton-Fisher, 2011) are coupled with an overall decrease in activity, this may not be indicative of a positive welfare change.

Freezing behaviour and reduction in activity may be associated with helplessness, which is where an individual has no expectation of a relationship between responses and outcomes (Ursin and Olff, 1993) and such a state is associated with high levels of anxiety (Gray and McNoughton, 2003). Thus overall reductions in activity in the face of environmental factors out of the animals' controls could be indicative of anxiety and helplessness. Increases in active social behaviours, such as playing and grooming, as well as a reduction of inactivity, aggression and abnormal behaviours would indicate that a form of enrichment is truly enriching the target animals.

Conclusion

Zoo-housed chimpanzees experience many aspects of zoo life that can potentially lead to them having poor welfare and their prevalence of abnormal and self-injurious behaviours is much higher than desired. Identifying the causes or triggers for these behaviours could help to minimize the stressors that lead to chimpanzees displaying these behaviours, reduce the occurrence of these behaviours and therefore improve the chimpanzees' welfare. However, so far it has not been possible to identify the trigger for R/R, a behaviour that may be indicative of poor welfare that zoos are very keen to remove from their chimpanzee populations but have not been able to do thus far. The provision of environmental enrichment can possibly improve chimpanzee welfare but currently many forms of enrichment are provided for animals with insufficient thought as to how the enrichment meets a behavioural need for the animal and the effectiveness of the form of enrichment is rarely tested. I believe that it is vital that any form of potential enrichment is rigorously tested to ensure it is having positive welfare effects on the target animals.

Thesis Outline and Aims

During the course of this thesis I conducted applied research that aimed to have direct implications for the improvement of zoos for both the welfare of chimpanzees and the education of human visitors.

Chapter 3 - Welfare of Zoo housed Chimpanzees (Pan troglodytes) with special attention to Regurgitation and Reingestion (R/R). This empirical chapter attempted to identify the causes of R/R in captive chimpanzees. I examined the possible daily triggers of R/R, as well as two self-directed behaviours, in a group of zoo-housed chimpanzees. I also looked at how long-term social and dietary changes may have affected group rates of R/R.

Chapter 4- Is Music Enriching for Group-housed Captive Chimpanzees (Pan troglodytes)? : Observational Research. This empirical chapter investigated the effectiveness of a commonly used form of enrichment for zoo-housed chimpanzees. Music is a form of sensory enrichment that is frequently used for captive chimpanzees but so far no research has been published on whether it has an enriching effect on the behaviour of zoo-housed chimpanzees.

Chapter 5 – Is Music Enriching for Group-housed Captive Chimpanzees (Pan troglodytes)? : Experimental Research. In this empirical chapter I investigated the efficacy of music as a form of enrichment for zoo and laboratory housed chimpanzees by providing devices that allowed the animals options of listening to different genres of music or silence.

Chapter 6 – Are 'Keeper Talks' effective at transmitting educational messages about environmental enrichment within zoos? This empirical chapter addressed the issue raised in chapter 1 that more research is required on assessing the effectiveness of zoo-based education. I investigated if 'Keeper Talks' led increases in zoo visitor knowledge via a questionnaire-based study and conducted interviews with zoo professionals to discuss their aims and how they are designed.

Chapter 7 – General Discussion. This chapter looked at how the results of chapter 3 to 6 can be applied within zoos and addressed the future of zoo based research.

Chapter 3: Welfare of Zoo-housed Chimpanzees (*Pan troglodytes*) with special attention to Regurgitation and Reingestion (R/R)

Abstract

In non-human primates, displacement behaviours, such as self-scratching and yawning, are considered markers of anxiety and stress and Regurgitation and Reingestion (R/R) is an abnormal behaviour, which has negative consequences for physical health and may be indicative of poor mental health. Previous studies suggest that R/R may be linked to boredom, sources of stress, type of food and limited opportunities to eat throughout the day. I aimed to examine the possible triggers of R/R, scratching and yawning in a group of zoo-housed chimpanzees. Firstly 20-minute focal observations were conducted on 18 adult chimpanzees at Edinburgh Zoo, UK, in addition to scan samples of visitor numbers and all occurrence samples of flash photography, screaming and banging on the glass in the exhibit. I analysed 158 hours of data and Generalised Linear Mixed Models revealed that yawning was significantly more likely if the period since the last feed was long, when enclosure windows were covered by a medium percentage of visitors and when there were medium numbers of visitors in the zoo. There were trends that yawning was more likely to occur if children screamed and that scratching was more likely to occur if visitors used flash photography. R/R occurred most within 40 minutes of a feed, but was not affected by the inter-feed interval preceding that feed, positive or negative social interactions or visitor numbers or behaviour. As there was no obvious daily trigger for R/R I conducted an analysis of long-term data, from 2009 to 2015, to investigate if social factors or dietary factors affected rates R/R over a longer timescale. It was found that R/R rates in the months before significant events including deaths of group members, the birth of an infant and a significant diet change were not different from R/R rates in the months after these events, but it was found that R/R rates decreased over the five year period. Lastly, I found no evidence that the introduction of individuals engaging in R/R lead to any of the resident chimpanzees habitually adopting the behaviour, despite considerable opportunities to observe it. These findings have implications for welfare interventions aimed to reduce R/R and/or anxiety behaviours in captive populations and for the translocation of individuals that are known to engage in R/R between groups.

Introduction

Keeping animals in captivity, which often represents a very different environment to the wild, has the potential to negatively impact upon animal welfare. Zoo environments present a unique set of challenges, with animals regularly exposed to high numbers of unfamiliar visitors, restricted space and unnatural social group compositions (Hosey, 2005). Whilst several other captive settings share some of these challenges, the effect of visitors on animal welfare is an issue unique to zoo settings and a substantial amount of research has focussed on assessing whether visitors create a challenge to zoo animal welfare (Hosey, 2000). Some evidence has been found that visitors have an enriching effect on captive primates; chimpanzees can interact positively with visitors (Cook and Hosey, 1995) and green monkeys (*Chlorocebus sabaeus*) are more likely to interact with visitors when visitor density is high (Fa, 1989).However, much of the evidence found implies that visitors negatively affect the animals. For example, mandrills (*Mandrillus sphinx)* exhibit higher levels of leg/hair pulling, stereotyped locomotion and masturbation in the presence of high visitor numbers (Chamove et al., 1988) and Fennec foxes (*Vulpes zerda*) show more stereotypic pacing (Carlstead, 1991).

In several studies it seems that it is not simply the presence of humans as such but their high numbers or behaviour that decreases welfare. One study on gorillas (*Gorilla gorilla gorilla*) at Belfast zoo found that when visitor density was low the gorillas showed behaviour indicative of relaxation and resting (Wells, 2005). However, when the visitor density was high they displayed stress related behaviours, such as intra-group aggression, body rocking and teeth clenching. This suggests that they were unable to escape the view of the public, leading to them becoming stressed when many visitors were present. Mitchell et al., (1992) attempted a multi-species study at Sacramento zoo on visitor effect. It was found that active groups of visitors (where at least one individual attempted to attract an animal's attention), regardless of size, induced more locomotion and audience directed behaviours than passive groups, although the authors do not state if they believed that was a sign of a positive or negative welfare change. If the presence of unfamiliar visitors in zoos is potentially having negative effects on the animals within the zoos then more research is needed into what exactly causes these effects and how they can be minimised.

More broadly, it is not only vital for animal welfare, but also valid research findings and the education of visitors that potential stressors in the zoo environment are identified and minimised. Visitors and researchers should have the opportunity to observe and learn from animals displaying natural behaviours, rather than high levels of anxiety-related or abnormal behaviours. For any given species it is thus important to identify and monitor anxiety-related and abnormal behaviours and what may trigger their performance.

In non-human primates, Self-directed Behaviours (SDBs) can be used to identify anxiety (Troisi, 2002) and abnormal behaviours can indicate mental health issues or suffering (Birkett and Newton-Fisher, 2011) that may be a result of captivity. It is essential that research into the triggers of these behaviours is conducted to inform strategies to help reduce these unwanted behaviours.

SDBs are behaviours that are believed to indicate short-term anxiety (Maestripieri et al., 1992) but if they are expressed frequently over a long period of time they can be considered a welfare issue. SDBs are often used to measure the emotional states of primates (Maestripieri et al., 1992) and are suggested to be coping mechanisms, as individuals that display SDBs have lower stress levels than those who do not (Higham et al., 2009). One of the most commonly seen SDBs is scratching (Mastriepieri et al. 1992). Scratching has been shown to be induced in Long-Tailed Macaques when given anxiolytic drugs (Schino et al., 1991), rates increase after aggression (Japanese Macaques: Schino et al., 1998) and in proximity to a dominant individual (Olive Baboons: Castles et al., 1998). Visitor effects can also alter scratching rates. It was found that when not given enrichment, high visitor numbers were associated with high rates of scratching in two groups of captive Gorillas (Carder and Semple, 2008). Yawning is another commonly observed SDB in primates (Maestripieri et al., 1992). Rates of yawning have been seen to increase in wild chimpanzees both during periods of social tension (Baker and Aurelli, 1997) and when in close proximity to humans (Nishida, 1970). As with scratching, yawning is also susceptible to visitor effects in captivity. In an Indian zoo, where the Lion-tailed macaques were often 'taunted' by visitors, yawning rates were higher when animals were 'on-exhibit' compared to when they were 'off-exhibit' (Mallapur et al., 2005).

Captive primates can engage in Regurgitation and Reingestion (R/R), yet is rarely seen in the wild, so is therefore considered an abnormal behaviour. It is believed to indicate previous stress or current distress. The behaviour is defined as the voluntary movement of food from the stomach or the oesophagus into the hand, the mouth or on to a substrate followed by the consumption of the regurgitant (Gould and Bres, 1986a). It is a behaviour that can lead to serious health issues; the same behaviour in humans, known as rumination (Nakanishi and Anderson, 1982) has been linked to health problems such as oesophageal strictures, ulcers, reflux, oesophagitis, intestinal obstruction, oesophageal motor disorders and pulmonary aspiration (Wyngaarden et al., 1992). As well as the impacts on the animals, it is a behaviour that is likely to be found to be unpleasant by zoo visitors (Ackers and Schildkraut, 1985) and could affect the educational potential of the exhibit by giving false impressions of the species (Carlstead, 1998; Ironmonger et al., 1992; Ackers and Schildkraut, 1985).

So far no studies have found a single trigger for R/R yet many possibilities have been suggested. Affiliative behaviour, including grooming, has been shown to have positive effect, decreasing R/R rates whilst aggression increased the rates of R/R in Bonobos (Miller and Tobey, 2012). Boredom has been put forward as a possible cause. Giving a foraging task involving straw lead to significant reduction in R/R in laboratory housed chimpanzees (Baker, 1997). Also, rates of abnormal behaviours, including R/R, decreased significantly when a familiar caretaker spent an additional 10 minutes per individual, five days a week, interacting with pair and trio housed laboratory chimpanzees (Baker, 2004). R/R is also thought to be affected by visitor presence and density in zoos. Significantly higher rates of abnormal behaviour, including R/R, were also found by Mallapur et al. (2005) in the lion-tailed macaques that were 'on exhibit' than off exhibit and by Wells (2005) in gorillas during periods of high visitor density compared to those with low visitor density. The final possible trigger for R/R is diet. Fruit and starchy vegetables have been found to increase R/R rates in laboratory chimpanzees and zoo-housed gorillas (Morgan et al., 1993; Lukas et al., 2014). Increasing the amount of time since eating has also been linked to higher R/R rates in chimpanzees (Baker and Easley, 1996).

Aims and Research Questions

I conducted two studies where the aims of the first were to identify the triggers of self-directed behaviours and R/R in a group of zoo-housed chimpanzees. In study two I aimed to examine how rates of R/R have changed over the past five years and what might have led to any changes, using longitudinal data.

For the first study I conducted an in depth investigation into the possible causes of SDBs and R/R within the group of chimpanzees at Edinburgh Zoo. It was hoped that if triggers were established then it could be possible to create strategies to mitigate these behaviours. Unlike previous studies I looked at all of the following possible causes; the effects of grooming, aggression, the length of time between feeds, the type of food the animals receive, density and numbers of visitors as well as if visitors displaying specific behaviours cause the animals to become anxious, which has not previously been studied.

In this study I aimed to address the following questions:

i) Does the density of visitors at the enclosure windows or the overall number of visitors in the zoo have an effect on rates of R/R and SDBs? Based on the results of Carder and Semple (2008), Wells (2005) and Mallapur et al. (2005) it was predicted that high visitor density and numbers would cause in an increase in rates of R/R and SDBs.

ii) Does the occurrence of specific behaviours by visitors affect the rates of R/R and SDBs? Whilst no studies thus far have investigated the effect of specific behaviours displayed by zoo visitors on the behaviour of zoo-housed chimpanzees, Mallapur et al. (2005) noted that behaviours such as shouting and teasing animals were common place in Indian zoos where the presence of visitors was found to increase rates of SDBs and abnormal behaviours. This led me to predict that zoo visitors displaying specific potentially negative behaviours would increase rates of SDBs and R/R.

iii) Does being involved in grooming or aggression affect rates of R/R and SDBs? I predicted, based on the findings of Miller and Tobey (2012), that being involved in grooming would decrease an individual's rates of R/R and SDBs whilst being involved in aggression would lead to the opposite.

iv) Does the length of time between feeding events affect rates of R/R and SDBs? It was predicted that SDB and R/R rates would increase when the time between feeds was long (Baker and Easley, 1996).

v) Does the type of food given to the chimpanzees affect rates of R/R? Based on the findings of Morgan et al. (1993) and Lukas et al. (2014), I predicted that fruit and starchy vegetables would increase rates of R/R.

Methods

Study Site

The study was undertaken at Budongo Trail Chimpanzee enclosure, Edinburgh Zoo, Scotland. The facility was built in 2008 and has capacity for 40 chimpanzees. The facility is over 1500m^2 and comprises of three indoor ‘pods’, a bedding area and an outdoor enclosure, all linked by tunnels. Each of the ‘pods’ and the outdoor area contain large, wooden climbing structures with built-in wooden climbing structures with built in metal baskets that can be used for day beds, encouraging natural bedding behaviours. This layout allows the animals to split into sub-groups that vary in composition of individuals, allowing their natural fission-fusion social system to be expressed. Budongo Trail receives approximately 800,000 visitors each year (Whitehouse et al., 2014).

Subjects

The group of chimpanzees at Edinburgh Zoo comprises of two sub-groups; individuals from Edinburgh and individuals that came from Beekes-Bergen Safari Park, The Netherlands (table 1). The latter were introduced in 2010 in the hopes of breeding pure-bred western chimpanzees (*Pan troglodytes versus*). Prior to being in the Beekes-Bergen Safari Park, these individuals were housed in a medical testing facility where their history was unknown.

Table 1 – Demographic information on Chimpanzees at Edinburgh Zoo

Name	ID	Sex	Age at Start of Study	Rearing	Original Group
Cindy	CI	F	49	Wild	Edinburgh
David	DA	M	38	Mother	Edinburgh
Edith	ED	F	16	Mother	Beekes Bergen
Emma	EM	F	33	Mother	Edinburgh
Eva	EV	F	34	Nursery	Beekes Bergen
Frek	FR	M	19	Mother	Beekes Bergen
Heleen	HL	F	21	Mother	Beekes Bergen
Kilimi	KL	F	20	Mother	Edinburgh
Kindia	KD	M	16	Mother	Edinburgh
Lianne	LI	F	24	Mother	Beekes Bergen
Liberius	LB	M	14	Mother	Edinburgh
Louis	LO	M	37	Wild	Edinburgh
Lucy	LU	F	36	Mother	Edinburgh
Paul	PA	M	19	Mother	Beekes Bergen
Pearl	PE	F	44	Wild	Beekes Bergen
Qafzeh	Q	M	21	Mother	Edinburgh
Rene	RE	M	20	Nursery	Beekes Bergen
Sophie	SO	F	33	Nursery	Beekes Bergen

Study 1: Short -term Data

Data collection

Data collection occurred over two study periods; 13th March 2014 to 8th July 2014 and 6th January 2015 to 2nd March 2015. 20 minute focal samples (Altmann, 1974) were carried out on all 18 adult individuals within the group. Data were collected on whether the focal individual was involved in grooming or aggression (including roles in these interactions) and if they yawned (Y/N), scratched (Y/N) or engaged in R/R (Y/N) during the focal period. During the focal period, all occurrence sampling of visitors using flash photography, banging on the windows of the enclosure and children screaming occurred. Before and after each focal, instantaneous scan samples (Altmann, 1974) were used to record the percentage of the windows of the focal pod that were covered by visitors from 0 to 100%, with 10% increments, and mean percentages of the windows covered by visitors from scans taken at the start and end of each focal were calculated. Unfortunately examination of the visitor behaviour and presence data through Q-Q plots and the acquisition of significant Shapiro-Wilk tests of normality indicated that they were not normally distributed. Attempts were made to transform the data but failed to produce normal distributions, due to the high frequency of scores at the extremes of our scales. Therefore, the variables were converted into categorical variables. The visitor behaviour data were converted into binary measures that indicating if these behaviours were present or absent during each focal period. Mean percentages of the windows covered by visitors were categorised into low (0-15%), medium (16-50%) and high (51%+) and gate numbers were categorised into low (0-1000), medium (1001-4000) and high (4000+) visitor numbers. The category boundaries for these two variables were chosen as they gave a roughly equal distribution of data in each category.

The keepers provided detailed records of the time, type and quantities of food given to the chimpanzees on a daily basis. Food data were categorised based on methods used in Plowman (2013) into starchy vegetables, fruit or neither. This was done based on the findings of Lukas et al. (2014) and Morgan et al. (1993), which suggest that these types of food may be triggers for R/R. If feeds were given that contained multiple food types, each type of food was categorised separately so there were multiple data points for that feed. To account for this, each feeding event was assigned a number so that different data points from the same feed had the same number for feeding event. Before data analysis was undertaken, it was noted that only six of the 18 chimpanzees were regularly seen to engage in R/R and the majority of these events happened within 40 minutes of the most recent feed (Figure 1). For these reasons, the data for all analysis of R/R came from just those six chimpanzees and focal samples that occurred within 40 minutes of a keeper feeding event.

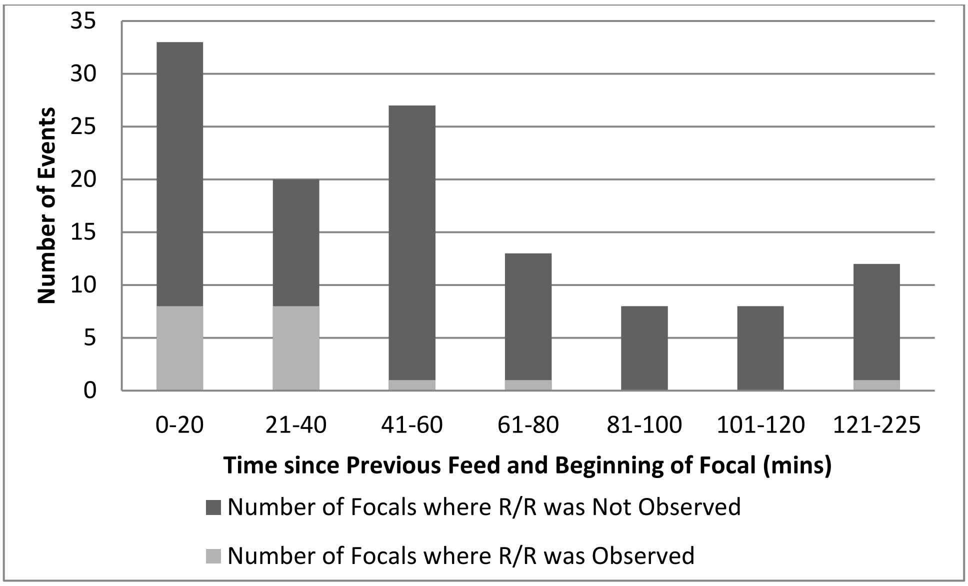

Figure 1 – Distribution of R/R events over time with the number of focals where R/R was not observed in dark grey and the number of those where R/R was observed in light grey

<u>Data Analysis</u>

Statistical Analysis

General Linear Mixed Models (GLMMs) with a binomial error structure and a logit link were used to investigate the influence of categorical and continuous explanatory variables on whether or not the chimpanzees displayed the behaviours in question. Individual identity was included as a random factor to address the issue of pseudoreplication due to each individual contributing multiple data points to the analyses. Likelihood ratio tests were run for full models and to determine the contribution of each variable in the model. If a factor that explained significant variation in dependent variable contained three categories, post-hoc GLMMs were run, only containing two of the three categories within the factor. All tests were run using SPSS v.21 with an alpha value of .05, but with Bonferroni corrected alpha levels of .017 applied to post hoc tests.

Do density and number of visitors affect the abnormal or stress behaviours of chimpanzees?

To test if visitor density or number affected R/R, scratching and yawning in the chimpanzees, I ran three Generalised Linear Mixed Models (GLMMs) where the dependent variable was whether or not the focal individual displayed the key behaviour (R/R, scratching or yawning [Y/N]), the independent variables were the level of windows in the focal pod covered by visitors (low, medium and high) and the level of visitor numbers present in the zoo on that day (low, medium and high) and the random effect was individual identity. For scratching and yawning, there were 474 focal sample data points from 18 chimpanzees (N= 18) and for R/R there were 68 focal sample data points from the only six chimpanzees that were known to R/R (N= 6)

Does visitor behaviour affect the abnormal or stress behaviours of chimpanzees?

To test if specific behaviours demonstrated by the visitors affected R/R, scratching and yawning in the chimpanzees I ran three GLMMs where the dependent variable was whether or not the focal individual displayed the key behaviour (R/R, scratching or yawning;[Y/N]), the independent variables were whether at any time during the focal sample a visitor used flash photography (Y/N), banged on the window of the focal pod (Y/N) or if a child screamed (Y/N) and the random effect was individual identity. For scratching and yawning, there were 474 focal sample data points from 18 chimpanzees (N= 18) and for R/R there were 68 focal sample data points from only the six chimpanzees that were known to R/R (N= 6)

Does involvement in aggressive events affect the abnormal or stress behaviours of chimpanzees?

To test if the focal receiving or giving aggression during the hour of observations affected R/R, scratching and yawning in the chimpanzees, I ran three GLMMs where the dependent variable was whether or not the focal individual displayed the key behaviour (R/R, scratching or yawning [Y/N]), the independent variable was whether the focal animal received or gave aggression at any time during the hour long observation period (Y/N) and the random effect was individual identity. For scratching and yawning there were 142 data points from 18 chimpanzees (N= 18) and for R/R there were 54 data points from only the six chimpanzees that were known to R/R (N= 6). The number of data points for these analyses were lower due as the exact time of aggression was not recorded, meaning that it was only possible to know if an aggressive event happened within the 60 minute observation period (the length of three back-to-back focal samples). As such, it was only possible to use the final focal sample collected within each hour-long observation period.

Does involvement in grooming affect the abnormal or stress behaviours of chimpanzees?

To test if the focal receiving or giving grooming affected R/R, scratching and yawning in the chimpanzees, I ran three GLMMs where the dependent variable was whether or not the focal individual displayed the key behaviour (R/R, scratching or yawning [Y/N]), the independent variable was whether the focal animal received or gave grooming at any time during the focal sample (Y/N) and the random effect was individual identity. For scratching and yawning there were 474 focal sample data points from 18 chimpanzees (N= 18) and for R/R there were 68 focal sample data points from the six chimpanzees that were known to R/R (N= 6).

Does length of time since being fed affect the abnormal or stress behaviours of chimpanzees?

To test if the length of time since being fed affected R/R, scratching and yawning in the chimpanzees, I ran three GLMMs. For scratching and yawning dependent variable was whether or not the focal individual displayed the key behaviour (scratching or yawning; [Y/N]), the independent variable was the length of time between the start of the focal period and the last recorded feeding event and the random effect was individual identity. There were 358 focal sample data points from all 18 chimpanzees (N= 18).

For R/R, as R/R mostly occurred when food was available during or shortly before the focal, I looked at if the duration between the most recent feed (within the last 40 minutes from the focal period) and the previous feed affected the occurrence of R/R. I ran a GLMM where the dependent variable was whether or not the focal individual was seen to R/R (Y/N), the independent variable was the amount of time between the most recent feeding event and the previous feeding event and the random effect was individual identity. There were 51 focal sample data points from the six chimpanzees that were known to R/R (N= 6).

The number of data points for these analyses were lower than previous analyses as for some focals the previous feeding event and the most recent feeding event had been on separate days. As it was not possible to be sure of what or if the chimpanzees had eaten overnight, these data points were not included in the analyses.

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

For this I ran a single GLMM. The dependent variable was whether or not the focal individual was seen to R/R (coded binomially), the independent variable was the type of food that was most recently provided (starchy vegetable, fruit or neither) and the random effects were individual identity and the number of the feeding event. There were 91 focal sample data points from the six chimpanzees that were known to R/R (N= 6). There were a greater number of data points for this analysis as there were multiple data points for some feeding events due to several types of food being given at the same time.

Results

Do density and number of visitors affect the abnormal or stress behaviours of chimpanzees?

Visitor density at the enclosure and visitor numbers in the zoo did not explain a significant amount of variation in whether R/R or scratching behaviour occurred (Table 2). In contrast, these factors did explain a significant amount of variation in whether the chimpanzees yawned (Table 2). Post-hoc GLMMs were run and found that a significantly higher proportion of focal samples contained yawning when there was medium percentage cover of windows compared to high percentage cover of windows. It was also found that a significantly higher proportion of focal samples contained yawning when there were medium zoo visitor numbers compared with low zoo visitor numbers (table 3).

Table 2 – Results of GLMMs on the effects of visitor density and number on R/R, scratchingand yawning. Significant results in bold.

Dependent Variable	Full Model F value (df)	p value	Percentage of the windows of the focal pod covered by visitors F value (df)	p value	Total numbers of visitors in the zoo F value (df)	p value
R/R	1.08 (4, 178)	.370	0.67 (2, 178)	.513	1.42 (2, 178)	.243
Scratching	0.77 (4, 469)	.546	0.002 (2, 469)	.998	1.52 (2, 469)	.220
Yawning	**11.75 (4, 469)**	**<.001**	**9.27 (2, 469)**	**<.001**	**15.95 (2, 469)**	**<.001**

Table 3 – Results of Post-hoc GLMMs on the effects of visitor density and number on yawning. Significant results are shown in bold.

Categories contained in the GLMM	Full Model F value (df)	p value	Percentage of the windows of the focal pod covered by visitors F value (df)	p value	Total numbers of visitors in the zoo F value (df)	p value
Low and Medium	**3.61 (2, 362)**	**.028**	0.40 (1, 362)	.529	**7.19 (1, 362)**	**.008**
Medium and High	**6.68 (2, 171)**	**.002**	**11.42 (1, 171)**	**.001**	1.03 (1, 171)	.312
Low and High	1.28 (2, 177)	.280	2.16 (1, 177)	.144	0.06 (1, 177)	.809

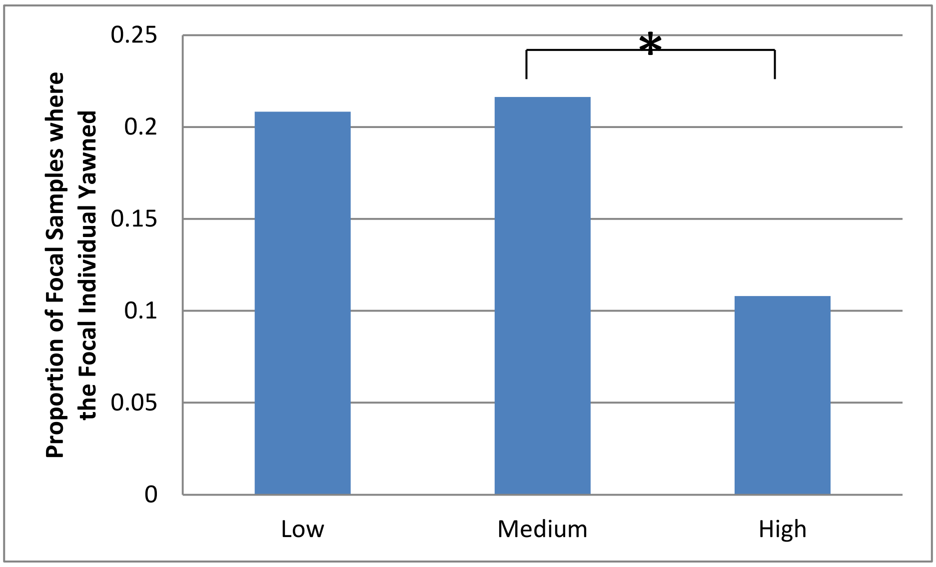

Figure 2 – The proportion of focal samples where the focal individual was seen to yawn when the percentage of windows covered by visitors were low (0-15%), medium (16-50%) and high (51%+).

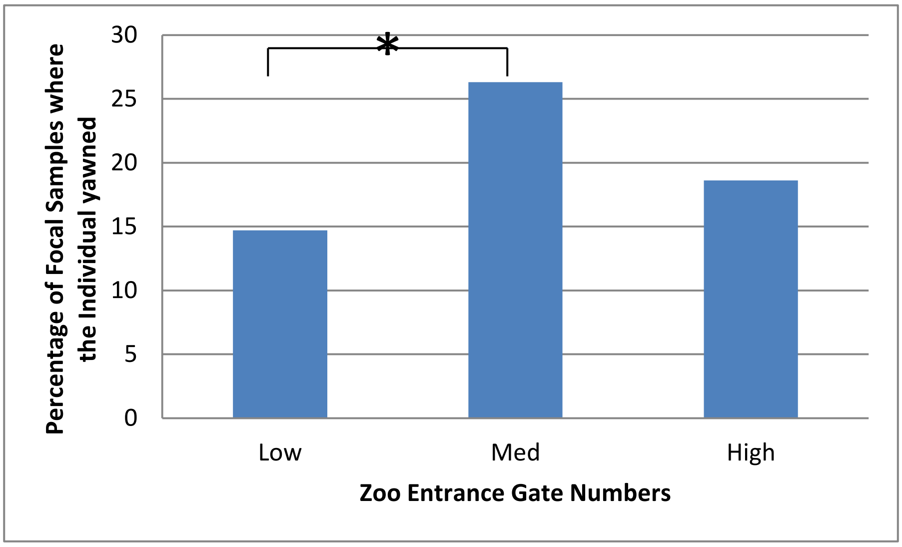

Figure 3 – The proportion of focal samples where the focal individual was seen to yawn when the Zoo entrance numbers were low (0-1000), medium (1001-4000) and high (4001+).

Does visitor behaviour affect the abnormal or stress behaviours of chimpanzees?

None of different types of potentially disruptive visitor behaviours explained a significant amount of variation in whether or not the chimpanzees engaged in R/R (Table 4).

Table 4 – Results of GLMMs on the effects of visitor behaviours on R/R.

Independent Variable	F value (df)	p value
Full Model	0.72 (3, 64)	.546
Banging on Windows	0.04 (1, 64)	.841
Camera Flashes	0.97 (1, 64)	.328
Children Screaming	1.25 (1, 64)	.268

Overall visitor behaviour did not explain a significant amount of variation in whether or not chimpanzees scratched (F (3, 470)= 1.56 p= .198). However, when individual factors within the model were examined, there was a trend for a higher proportion of focal samples to contain scratching when flash photography was used than when it was absent (F (1, 470)= 3.59 p= .059; Figure 4). Children screaming (F (1, 470)= 0.003 p= .957) and visitors banging on the windows (F (1, 470)=0.46 p= .496) did not explain a significant amount of variation in whether or not chimpanzees scratched.

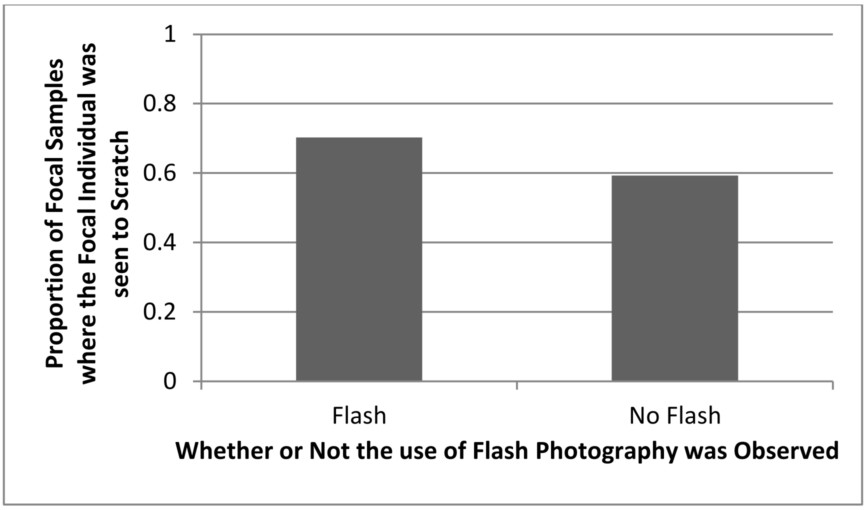

Figure 4 – The proportion of focal samples where the focal individual was seen to scratch when flash photography was used by visitors and when it was not.

Overall visitor behaviour did not explain a significant amount of variation in whether or not chimpanzees scratched (F (3, 470)= 0.10 p= .395). However, when individual factors within the model were examined, there was a trend for a higher proportion of focal samples to contain yawning when children screamed than when they did not (F (1, 470)= 2.98 p= .085;

Figure 5). Flash photography (F(1, 470)= 0.003 p= .956) and visitors banging on the windows (F(1, 470)=1.67 p= .198) did not explain a significant amount of variation in whether or not chimpanzees yawned.

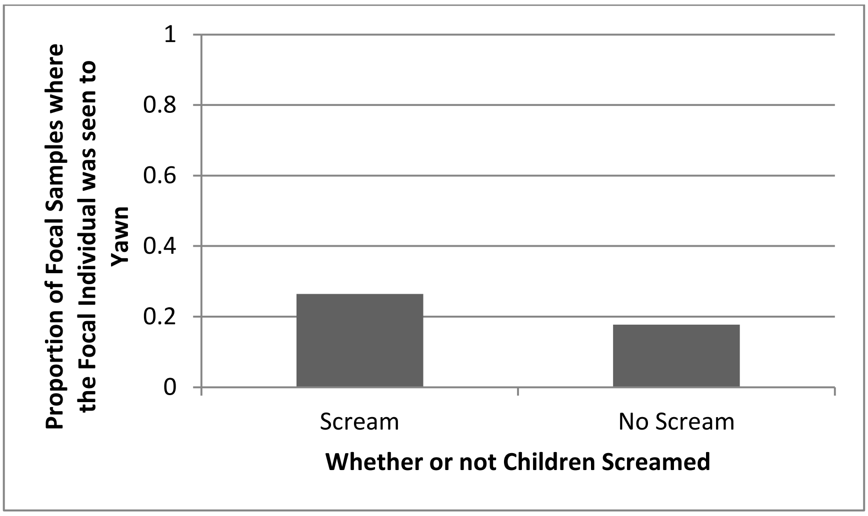

Figure 5 – The proportion of focal samples where the focal individual was seen to yawn when children screamed and when they did not.

Does involvement in aggressive events affect the abnormal or stress behaviours of chimpanzees?

Receiving or giving aggression at any time during the focal period did not affect whether or not the chimpanzees engaged in R/R, scratched or yawned (table 5).

Table 5 – Results of the effect of involvement in aggressive events on R/R, scratching and yawning.

Dependent Variable	Receiving or Giving Aggression F value (df)	p value
R/R	0.04 (1, 52)	.844
Scratching	0.03 (1, 140)	.855
Yawning	0.12 (1, 140)	.726

Does involvement in grooming affect the abnormal or stress behaviours of chimpanzees?

Receiving or giving grooming at any time during the focal period did not affect whether or not the chimpanzees engaged in R/R, scratched or yawned (table 6).

Table 6 – Results of the effect of involvement in grooming on R/R, scratching and yawning

Dependent Variable	Receiving or Giving Grooming F value (df)	p value
R/R	2.51 (1, 181)	.115
Scratching	1.04 (1, 181)	.309
Yawning	0.49 (1, 181)	.486

Does length of time since being fed affect the abnormal or stress behaviours of chimpanzees?

The amount of time from the most recent feeding event did not affect whether or not the chimpanzees scratched ($F(1, 355)= 0.08$, $p= .783$), whereas the amount of time from the most recent feeding event did effect whether or not the chimpanzees yawned ($F(1, 355)= 5.30$ $p= .022$). Figure 6 shows that there were more focals that included yawning when the time between feeding events was longer. The amount of time between the most recent feeding event and the previous feeding event did not affect whether or not the chimpanzees engaged in R/R ($F(1, 49)= 1.63$, $p= .208$).

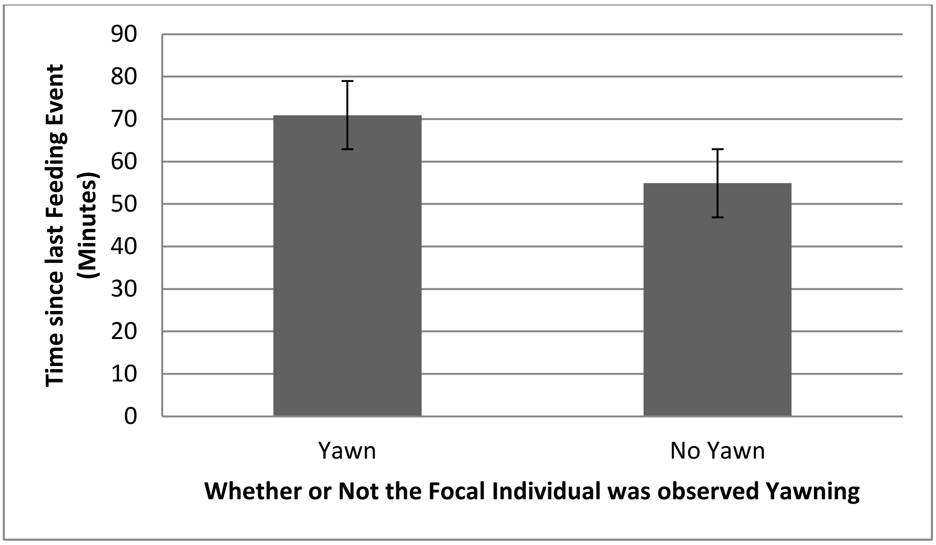

Figure 6- The mean duration in minutes from the last feeding event to the start of the focal samples where the focal individual was seen to yawn and not yawn. Error bars show Standard Error.

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

The type of food given did not affect R/R $F (2, 88)= 1.05$ $p= .354$.

<u>Discussion</u>

The main finding of this study is that, contrary to the predictions, few of the potential triggers we examined significantly affected the occurrence of SDBs or R/R within this group of chimpanzees. It is possible that the lack of triggers for scratching and R/R could be due to the design and layout of Budongo Trail, which allows the chimpanzees to engage in natural 'fission-fusion' dynamics.

A unique feature of this study was that it was the first to examine the possible effects of specific visitor behaviour on that of a group of zoo-housed chimpanzees. Previous studies have found that the activity or noise level of visitors negatively affects the behaviour of captive primates (Hosey and Druck, 1987; Chamove et al., 1988, Birke, 2002). I found trends that suggest that the use of flash photography or the presence of screaming children can increase SDBs in chimpanzees.

Several studies have shown that high visitor density can negatively affect behaviour (Wells, 2005; Birke, 2002; Skyner et al., 2004) leading us to predict that having a high percentage of exhibit windows covered by visitors would lead to an increase in SDBs. However, there was a greater proportion of focals that included yawning when there was a medium level of window coverage (16 to 50%). In contrast to the prediction, there was a higher proportion of focal sample where the focal animal was seen to yawn when there were medium zoo gate numbers (1001 to 4000 people), rather than high visitor numbers. These results are unexpected and show that further research into other associated factors, such as duration of visitor stay at enclosure windows and visitor noise levels, are required to establish what is driving these effects.

Another unexpected result was that neither grooming nor aggression seemed to have any effects on rates of SDBs. This contrasts with work on long-tailed Macques (Schino et al., 1988) and Crested Black Macaques (Aureli and Yates, 2010). However, my results are similar to Semple et al.'s, (2013) findings for scratching and grooming in Barbary Macaques. Semple et al. suggest that when the macaques terminated a grooming event it may have led to an increase in anxiety, which counter-acted the positive, anxiety reducing effect of grooming that would have been expected to lead to a reduction in scratching. In terms of our aggression results, the multiple 'pods' within the enclosure allowed the possibility of escaping aggression quickly or avoiding certain individuals: these alternative coping mechanisms could have reduced the need for SDBs.

A factor of the captive environment that this study has found to contribute to increases in SDBs was the period of time between feeding events. In the wild, chimpanzees spend 6.68 hours per day foraging or eating (Leonard and Robertson, 1994) whilst in captivity this is greatly reduced and can mean that there are long periods of time between feeding events. My results show that when the chimpanzees have to wait a long time they are more likely to yawn. The daily schedule of zoo keepers is already very full so it may not be possible to add in extra feeding times for the chimpanzees but automatic feeders that release food at specific times or random intervals could help negate this issue.

This study did not identify any potential triggers for R/R in this group. Previous research has suggested that the type of food given to the chimpanzees (Morgan, 1993) and increased time between feeds (Baker and Easley, 1996) can affect this behaviour, however, this was not found to be the case with this group of animals. The average rate of R/R from my data was 5.7%, which seems comparable with the rate of 6.7% found by Birkett and Newton-Fisher (2011) and 5.4% by Kalcher-Sommersguter et al. (2013). This suggests that further research into R/R within this group should be undertaken and highlights that results with single groups of animals with abnormal behaviours, that may be a result of individual histories, may not be generalisable.

Study Two: Long-term Data

Aims and Research Questions

As I did not find any concurrent, daily factors that influenced R/R rates in study 1 (2014-15), I wanted to investigate whether the occurrence of rarer significant events affected R/R rates over a longer time period. More specifically I aimed to examine if the translocation and integration into a new social group, the births or deaths of group members and major diet changes affected the rates of R/R. Lastly, I examined the stability of R/R rates from 2009 to 2015. I focussed these analyses on the 11 chimpanzees who were integrated into the Edinburgh group in 2010 and who had relatively high levels of R/R behaviour at their previous facility, (Beekes-Bergen Safari Park (BB)). In addition, given that anecdotal reports from keepers and researchers indicated that the original Edinburgh individuals did not engage in R/R prior to the arrival of the BB group, I wanted to test whether this behaviour spread through social learning, as has been suggested for coprophagy (Hopper et al., 2016).

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

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

(ii) Are any changes in R/R rates related to changes in the diet given to the chimpanzees? Changes in the chimpanzees' diet, as recommended by zoo veterinarians and nutritionists in order to improve the digestion of the Beekes-Bergen individuals, may have led to changes in R/R rates.

(iii) Did the deaths or births of individuals affect R/R rates? I predicted that the deaths of members of the group would cause R/R rates to increase, based on the negative reactions of group members after the death of an individual recorded in Stewart et al. (2012) and Van Leeuwen et al. (2016). However, I predicted that the birth of a new individual would lead to a decrease in R/R rates, as group members often show interest in new infants (Goodall, 1986) and the infant may thus have reduced boredom.

(iv) Have R/R rates in BB individuals changed over time? Being integrated into a large and socially complex group living in an enclosure designed to encourage natural behaviours, such as ‘fission-fusion’ dynamics, in addition to several small diet changes over this period could have led to reductions in the BB individuals’ rates of R/R.

(v) Has observing R/R in the Beekes-Bergen individuals caused the Edinburgh Zoo individuals to adopt the behaviour? I predicted that R/R might be socially learnt, as it has recently been suggested that coprophagy may be (Hopper et al., 2016), which would mean that observing the Beekes-Bergen individuals engaging in R/R could lead to the performance and adoption of the behaviour by the Edinburgh Zoo individuals.

Methods

The data used in this longitudinal study came from University of York students working on independent research projects in 2010 and 2011 as well as a long-term dataset instigated in 2012. This dataset has been contributed to by all researchers conducting independent research projects at Budongo Trail who had to pass an identification test before they were able to contribute data. All researchers had to contribute a minimum of two hours of data per week. Researchers were regularly monitored and given feedback on data collection to ensure reliability. The data used for this study were collected from January 2009 to February 2015. Data were collected using 10 minute focal scans of individuals (Altmann, 1974) where all instances of R/R were recorded, along with details of which other chimpanzees were in the same pod as the focal animal and which of those were within 3 meters of the focal individual at the time of each R/R event. Some focals were interrupted before the end of the 10 minutes and these incomplete focal samples were not included in analysis. After data were collected we coded the R/R data binomially as whether or not R/R occurred during the focal sample. Data on changes to diets and the dates of the integration process were obtained from the keepers.

Data on the BB individuals prior to their arrival at Edinburgh Zoo was collected at Beekes-Bergen Safari Park from May 2009 to September 2009. 10 minute long focal samples (Altmann, 1974) were used to record the duration of time spent engaging in R/R by the focal individual. To make the data comparable to the Edinburgh Zoo data, each focal was scored for whether or not at least one R/R event occurred in the 10-minute time period.

Data Analysis

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

Monthly rates of R/R for the BB individuals were again used but were split into three time periods: pre-integration of the BB individuals (May to September 2009), during the integration (May to July 2010) and immediately after integration (August to December 2010). A Friedman test (N= 10) was used to compare the average rates of R/R for the three time periods.

Are the changes to R/R rates related to deaths or births?

For examining the effect of both births and deaths, individual averages of R/R rates were taken across the four months before and after each event. Each individual had to be present in at least six focal samples before and after each event to enter the analyses. Wilcoxon tests were run for Bram's death (N= 10), for Lyndsey's death (N= 9) and Velu's birth (N= 9).

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

The monthly R/R rates for the BB individuals, as described above, were used to compare the average R/R rates of the three months before and after a major diet change. On 20th October 2010 an additional 50kg of grapes, pears and mangos, 15kg of apples and four loaves of white bread were included in the weekly diet of the 22 animals. The criterion for inclusion into this analysis was that an individual had to have been observed for a minimum of 18 focal samples (three hours) during each three month period. A Wilcoxon test (N= 10) was used to compare the mean of the three monthly R/R rates, for each BB individual, before and after the diet change.

Have R/R rates changed over time?

Individual rates of R/R per month for the BB individuals were calculated by dividing the total number of focals each individual were seen to engage in R/R by the total number of focals each individual was observed. Only individuals that were present in the group for all seven years were included in this analysis (2 individuals were excluded due to deaths in this period). For each year, from 2009 to 2015 (N= 7), a yearly rate of R/R for each individual was calculated as a mean of the 12 monthly R/R rates. The group level annual mean R/R rate for each year was calculated as a mean of all seven individual yearly mean rates of R/R. The relationship between time and R/R rates was examined using a Kendall's-tau correlation, due to the small sample size.

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

In order to assess whether EZ individuals had potentially socially learnt to R/R, I first needed to estimate the minimum number of opportunities each EZ individual likely had to observe the behaviour in BB individuals from July 2010 to February 2015. I then examined the number of times the EZ individuals were recorded engaging in R/R during focal samples over the same time period.

In order to estimate the total number of R/R events observed by the EZ group since the arrival of BB individuals I first had to estimate the total number of R/R events the BB individuals engaged in during that period. This was done by dividing the total number of recorded R/R events by the total number of focals for BB chimpanzees to obtain the proportion of focal samples where individuals engaged in R/R. This proportion was then multiplied by 6 to find the hourly rate, (focal samples were 10 minutes long), which was then multiplied by 12 to obtain the daily rate (based on the assumption that the chimpanzees were active for 12 hours). The daily rate was then multiplied by 2190, which was the number of days during the six year period, to obtain the estimated number of R/R events during that time. Then, to estimate the chances of each EZ individual observing those R/R events, the proportion of BB R/R events each EZ individual observed within 3m was calculated (total number of focal samples where each EZ individual was within 3m of a BB chimp engaging R/R was divided by the total number of recorded R/R events). This proportion was then multiplied by the estimated number of R/R events over the six year period to obtain the estimate of the minimum total number of R/R events observed by the EZ since arrival of BB individuals.

Statistical analysis

All tests run were two-tailed with alpha level set at 0.05 and Bonferroni corrected to p= .017 for post hoc tests. Wilcoxon Signed Ranks, Friedmans and Kendall's-tau tests were run using SPSS v.21. Effect sizes (*d and r*) were calculated using an online tool (http://www.uccs.edu/~lbecker/). When using Cohen's *d* as an effect size, a large effect would be considered 0.80 and above, a medium sized effect would be 0.50 and 0.20 would be a small effect (Cohen, 1992). *r* was used as an effect size for non-parametric Wilcoxon

Signed Rank tests and a large effect would be 0.50 and above, 0.30 and above is a medium effect and 0.10 is a small effect (Pallant, 2007).

Results

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

There were significant differences between the rates of R/R over the three time periods examined: before the integration), during integration and after the integration (Friedman $X^2(2)= 9.60$ N= 10 p=.008; figure 7). Using Bonferroni corrected alpha levels, post-hoc Wilcoxon signed ranks tests show that the rates of R/R were significantly higher in the pre-integration condition than during post-integration (Z= -2.38, p=.017; *r*= 0.24). There were trends for the rates of R/R being higher during pre-integration than in the integration condition (Z= -2.24, p=.025; *d*= 0.22) and in integration than post-integration (Z= -2.20, p=.028; *d*= 0.22). Figure 8 shows how the proportion of focal samples including R/R changed for 10 of the BB individuals during the integration process and that all individuals contribute to the overall group decrease rather than one individual driving it.

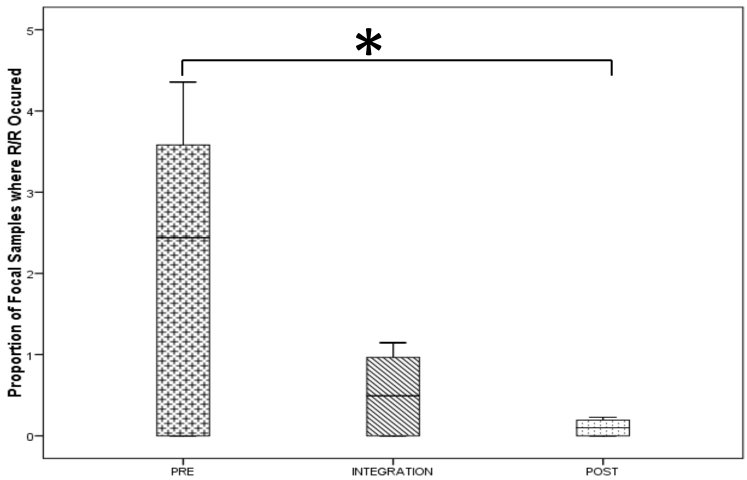

Figure 7 – Boxplot showing the median rates of R/R in BB individuals before, during and after integration of the BB individuals to Edinburgh Zoo

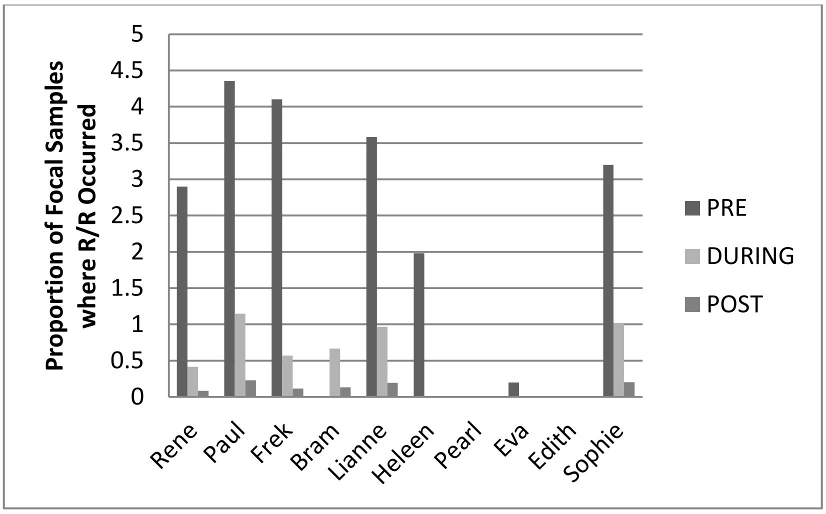

Figure 8- The individual median rates of R/R for the 10 BB individuals throughout the integration process

Are the changes related to births or deaths in the group?

R/R rates of BB individuals did not change significantly between the four months before and after Bram's death (N=10), Lindsay's death (N=9) or Velu's birth (N=9; table 7).

Table 7 – Results for Wilcoxon tests run to compare median rates of R/R before and after three major changes in the composition of the group.

Event (date)	Median for Four Months Before Event (IQR)	Median for Four Months After Event (IQR)	N	Z score	p value	*R*
Bram's death (2nd December 2010)	0.13/hour (0.73)	0.37/hour (1.37)	10	-1.54	.123	0.15
Lindsay's death (28th February 2013)	0.00/hour (0.56)	0.00/hour (0.33)	9	0.67	.500	0.07
Velu's birth (24th June 2014)	0.00/hour (1.00)	0.00/hour (0.42)	9	0.97	.360	0.10

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

R/R rates were not significantly higher after the diet change than before (Wilcoxon Z= -1.63 N= 10 p=.102; *r*= 0.16; figure 9).

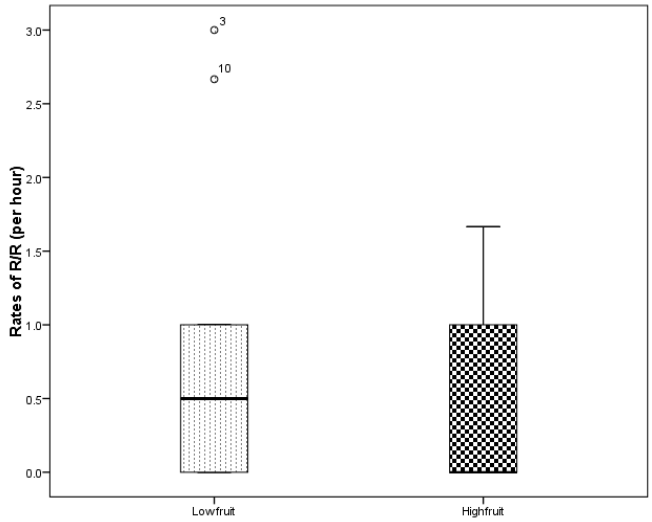

Figure 9 – Boxplot showing the median rates of R/R before and after the diet change

Have the R/R rates of BB individuals changed over time?

There was a trend for the rates of R/R decreasing over the period from 2009 to 2015 (τ_b = -0.62, *n* = 7, *p*= .051) (figure 10). Figure 11 shows how rates of R/R change over time for nine BB individuals and that all individuals contribute to the overall group decrease rather than one individual driving it.

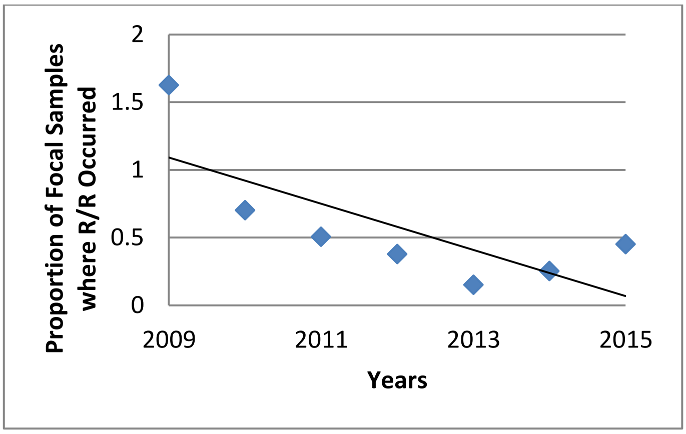

Figure 10 – The mean proportion of focal samples where R/R occurred each year for the nine BB individuals present in the group 2009-2015 with line of best fit.

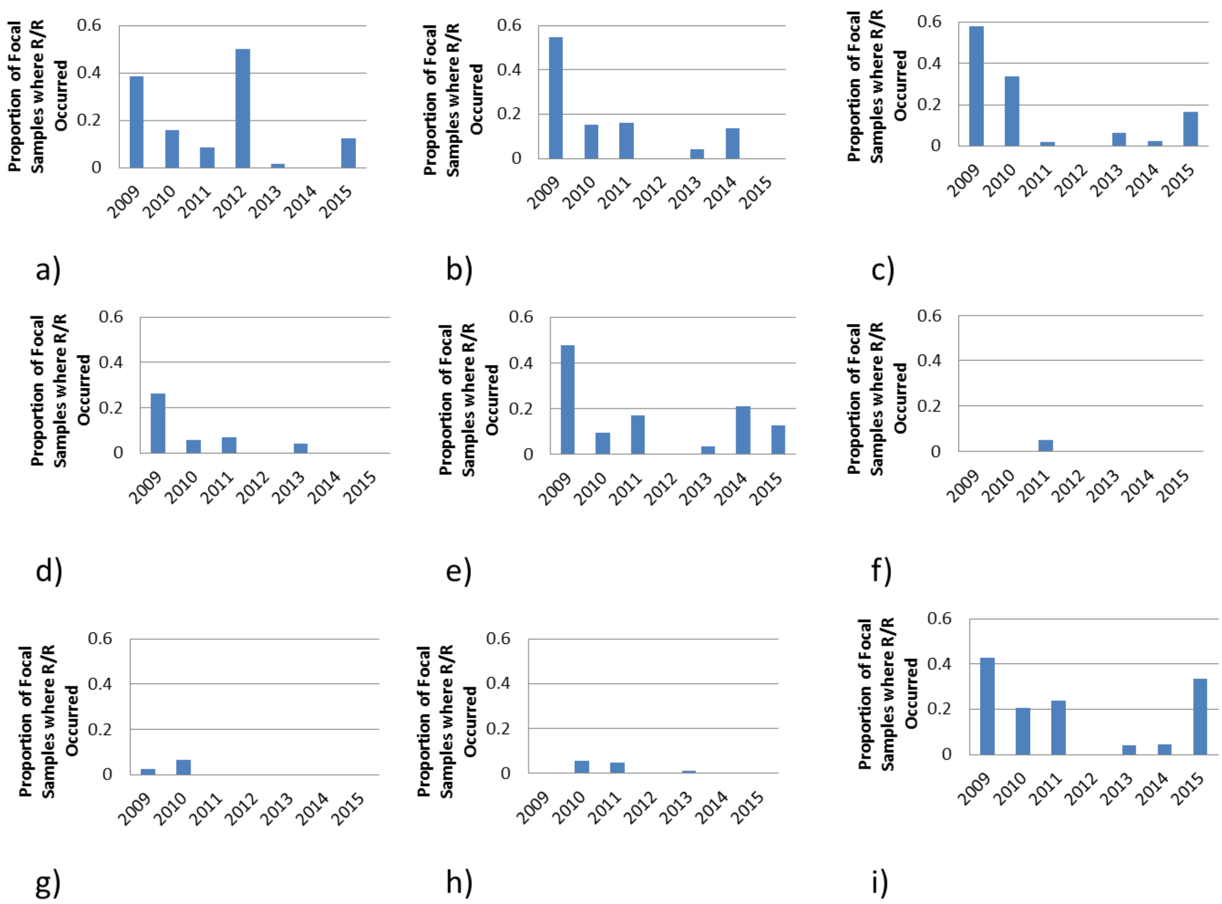

Figure 11 – Bar graphs showing the proportion of focal samples where R/R occurred for each of the years from 2009 to 2015 for each of the BB individuals present in the group during the whole of that time period. Illustrated are the rates for a) Rene, b) Frek, c) Paul, d) Heleen, e) Lianne, f) Pearl, g)Eva, h) Edith and i) Sophie.

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

Table 8 shows that despite the EZ individuals observing potentially as many R/R events as 1473 over six years, no individual was ever seen to engage in R/R themselves more than four times between August 2010 and February 2015. Figure 12 shows that the number of R/R events by the EZ individuals is low and sporadic between October 2010 and July 2013.

Table 8 – The number of observed R/R events by EZ individuals compared with estimates of the number of times each has observed R/R from July 2010 to February 2015. The observation time for Ricky and Lyndsay are much lower than other individuals as they died in 2012 and 2013 respectively.

ID	Total Estimated Observations of R/R since arrival of BB individuals in 2010	Total number of focal samples where EZ individuals were recorded engaging in R/R	Total observed Focal hours for EZ individuals
Ricky	173	1	14.33
Qafzeh	520	2	29.33
Kindia	1473	2	32.16
Louis	780	1	28.83
Liberius	260	0	34.00
David	520	4	28.50
Emma	693	1	30.00
Lucy	607	0	30.33
Lyndsay	347	3	15.00
Cindy	1214	2	33.67
Kilimi	780	2	32.00

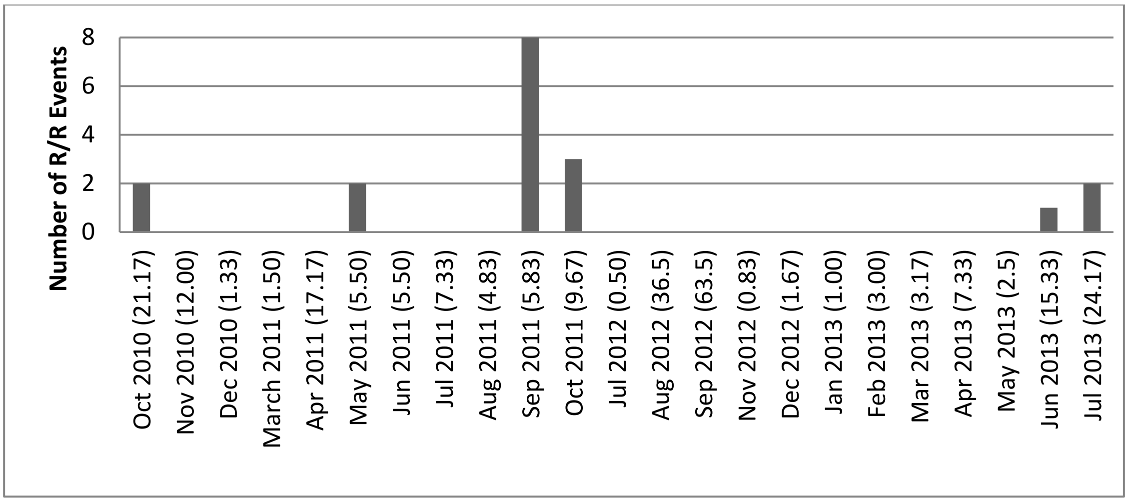

Figure 12 – R/R events by the EZ individuals per month with the number of hours of focal sampling during that month in brackets

Discussion

By looking at the rates of R/R before, during and after the integration of the BB chimpanzees into Budongo Trail the rates did not change as predicted. It was predicted that R/R rates would increase during the introduction between the two groups of individuals as this was believed to be a stressful time for the animals. However, R/R rates were significantly higher before the introduction. This suggests that the integration process, described in Schel et al. (2013), was perhaps not as stressful for the animals as predicted. It is also possible that R/R in the BB individuals is related to boredom and that the cognitive challenge presented by the introduction to a new physical and social environment may have reduced their boredom and, therefore, their rates of R/R. Previous studies have found that the provision of foraging related enrichment (Baker, 1997) and increased human caretaker interaction (Baker, 2004) has led to reductions in R/R rates. It is therefore recommended that further research investigating the link between boredom and R/R should be undertaken.

I predicted that changes to the rates of R/R could have been influenced by major changes to the social composition of the group that happened after the integration of the BB individuals. However, there were no significant differences between the rates of R/R before and after any of these events. Despite the stressful reactions to the deaths of an adult group members reported by Stewart et al. (2012) and Van Leeuwen et al. (2016), the lack of change to R/R rates is comparable to Anderson (2011) who reported no behavioural changes within the group after the deaths of group members. Contrary to my predictions, the birth of Velu was also not found to have significantly affected the rates of R/R. It was expected that the presence of a new infant in the group could have been enriching for all the individuals and potentially reduced R/R rates. However, as R/R rates were already low by 2014 (figure 7), it is possible that it was very difficult to be able to detect any difference that this birth might have made.

In October 2010, the diet of the chimpanzees was changed and the amount of fruit given weekly was increased. Based on the results of Morgan et al. (1993) it was predicted that this would lead to an increase in R/R. However, comparing the rates of R/R three months either side of this diet change showed there was no significant difference but this could have been because rates were already low before the change (mean of 0.50/hour for the three months prior). There were other small changes to the diet of these chimpanzees from April 2010 onwards but we lacked data to examine three months prior to and after each of these changes. It is possible, therefore, that each of these small changes may have contributed to the overall reduction in R/R rates within the BB individuals.

By looking longitudinally at the rates of R/R within the chimpanzees at Edinburgh Zoo I have been able to identify that the BB individuals' R/R rates have a trend for reducing over time, which indicates an improvement in their welfare. Some individuals (Pearl, Edith, Eva and Heleen) are no longer observed engaging in R/R. The design of Budongo Trail and being part of the large, socially complex group of chimpanzees is the most probable cause of the reduction of R/R rates since 2009 in the BB individuals. The fact that six of the animals still occasionally engage in R/R is likely due to the persistent nature of the behaviour. In humans, the same behaviour, known as rumination (Nakanishi and Anderson, 1982), has been linked to periods of distress in individuals of average intelligence and the behaviour is very difficult to eradicate (Nakanishi and Anderson, 1982). Whilst we do not know the history of the BB animals during their time in the medical testing facility, it is likely that the experience may have been stressful and this is where they first performed R/R. Once established as a behaviour pattern, as in humans, it may be difficult to eliminate, hence why the BB individuals still perform the behaviour, albeit at much lower levels.

It was predicted that R/R might be socially learnt, as it is suggested coprophagy may be (Hopper et al., 2016).Whilst nine of the 11 EZ individuals were recorded as engaging in R/R, only 18 instances were observed between July 2010 and February 2015. This is despite each individual having possibly observed as many as 1473 R/R events during the same time period. The first recorded instances of R/R by EZ individuals were during October 2010 and they were seen infrequently until 2013, after which time the behaviour seemingly disappears. As there is no empirical data on the existence or prevalence of R/R in the EZ animals prior to July 2010, it is possible that the behaviour was present during this time but unobserved by the keepers and researchers, possibly due to very low rates of the behaviour, that can be performed subtly and very quickly . Despite having ample opportunity to observe the behaviour being displayed by the BB chimpanzees, the behaviour was not adopted and performed at high rates by any EZ individual. This study demonstrates that the integration of individuals that engage in R/R into an established group that does not regularly display the behaviour does not seem to lead to the spread of the behaviour.

Conclusions

These two studies suggest that the use of flash photography by visitors and children screaming may cause short-term anxiety for the chimpanzees. I recommend further investigation into the effects of these visitor behaviours at Edinburgh Zoo and other zoos that house chimpanzees. No obvious trigger for R/R within this group of chimpanzees has been identified and whilst rates of the behaviour have reduced over time, this does not seem to be related to major diet changes or social events but may be due being part of a socially complex group in a well-designed enclosure. I suggest that future studies on the link between R/R and boredom are undertaken. I also suggest that R/R is unlikely to be a behaviour that is socially learnt and therefore movement of chimpanzees known to engage in this behaviour should not be ruled out due to concerns of the behaviour being spread.

Chapter 4: Is Music enriching for group-housed captive chimpanzees? – Behavioural Observations

Abstract

Many facilities that house captive primates play music for animal enrichment or for caregiver enjoyment. Previous studies of use of music as enrichment with chimpanzees (*Pan troglodytes*) have suggested positive behavioural effects of music, however, due to the subjects not being able to avoid the music, I feel that the results may have been interpreted incorrectly. I conducted two studies with zoo-housed chimpanzees investigate the effects of classical and pop/rock music on various variables that may be indicative of increased welfare. Study one compared the behaviour and use of space of 18 animals when silence, classical or pop/rock music was played into one of several indoor areas. Overall, chimpanzees did not actively avoid the area when music was playing but were more likely to exit the area when songs with higher beats per minute (BPM) were broadcast. Chimpanzees showed significantly fewer active social behaviours when music, rather than silence, was playing. They also tended to be more active and engage in less abnormal behaviour during the music but there was no change to either self-grooming or aggression between music and silent conditions. The genre of music had no differential effects on the chimpanzees' use of space and behaviour. In the second study, continuous focal observations were carried out on three individuals with relatively high levels of abnormal behaviour. No differences in behaviour between music and silence periods were found in any of the individuals. These results suggest that music does not have any profoundly positive welfare effects on the behaviour of chimpanzees, as suggested by previous research, but does not have any strong negative welfare effects either. If music is played for caregiver enjoyment, music with less than 90 beats per minute should be played preferentially.

Introduction

Environmental enrichment is a commonly used method for improving animal welfare. A major goal of enrichment is to simulate the activities of their wild counterparts and encourage species-typical behaviours (Mellen and Sevenich MacPhee, 2001). Successful enrichment often entails encouraging greater diversity of behaviours (Forthman-Quick, 1984) and more positive active behaviours, such as foraging for food. One inexpensive, durable form of enrichment that is currently used in many zoos is auditory enrichment and a 2006 European Directive recommends it's use for laboratory primates (Appendix A of European Convention for the Protection of Vertebrate Animals used for Experimental and other Scientific Purposes, 2006).

One method of assessing the success of a form of enrichment is how much the target animals use it. However, as discussed in chapter 2, I feel that for the purpose of these studies in order to be able to classify music as a form of auditory enrichment it must be seen to have a positive effect on animal welfare by reducing negative or abnormal behaviours and increasing positive forms of activity.

Music has been reported to be enriching for laboratory housed chimpanzees, with one study finding that five genres of music described by the authors as 'relaxing' (classical, country, ethnic, oldies and soft) together reduced aggression and abnormal behaviours as well as increased social grooming (Howell et al., 2003). However, these positive changes were also coupled with an increase in inactive behaviours. In this study, the chimpanzee could not choose to avoid the music, therefore, it is possible that the animals were responding to the music in a helpless manner. Videan et al., (2007) also found that music increased social interactions and decreased aggression in laboratory chimpanzees but rather than looking at differences in genre of music, the instrumentation of the music was manipulated. From this, they found that music solely comprised of instruments had a greater effect on increasing social interactions, whereas music including human vocals, especially that with slower tempos (50 to 90 beats per minute) was better at reducing aggression. The results of Howell et al., (2003) and Videan et al., (2007) suggest that music could have an enriching effect on chimpanzees. However, in both of these studies the animals were not given the option to avoid the music, meaning the observed changes in behaviour could have been part of a coping strategy for this uncontrollable situation and the behavioural changes observed were not indicative of positive welfare changes.

To date, music as enrichment has been studied with gorillas (*Gorilla gorilla gorilla*; Wells et al., 2006; Robbins and Margulis, 2014), orangutans (Ritvo and MacDonald, 2016) and gibbons (*Hylobates moloch*; Wallace et al., 2013) in zoos but chimpanzees have only been studied in a laboratory setting (Howell et al., 2003; Videan et al., 2007). As such, it is very possible that it is actually the case that music is not enriching for captive chimpanzees and should not be used as a form of enrichment for the species.

In this study we aimed to assess if music is actually enriching for captive chimpanzees by investigating the impact of music on the behaviour of captive chimpanzees whilst giving them the option to avoid the music if they desired. We also directly compared the effects of classical music with contemporary Pop/rock music, which animals may be exposed to inadvertently through music played for the enjoyment of care staff. Studies 1 and2 were conducted with 18 chimpanzees at Edinburgh Zoo.

Study 1: Whole Group Observations

Aims and Research Questions

This study aimed to examine if the presence of music affected the chimpanzees' use of space and their general behaviour. In contrast to previous studies, the enclosure design at Edinburgh Zoo meant that if music was played into just one area it was possible for individuals to avoid the music in one area while the music was played in another area if they chose to do so.

I aimed to address the following questions : (i) Does the presence of music in part of the enclosure affect the animals' use of space; do they approach or avoid the area where music is playing?, (ii) Does music affect the behaviour of the individuals exposed to the music? I predicted that if music was having a positive impact on welfare I would find increases in social and active behaviours combined with decreases in aggression and abnormal or stress related behaviours; and (iii) Do classical music and Pop/rock music have differing effects on the use of space and behaviour of the animals? Previous studies have shown that instrumental classical music reduces aggression and increases social grooming in laboratory chimpanzees (Videan et al., 2007) suggesting that the classical music in this study may have positive effects.

Methods

Ethics Statement

The procedure was approved by the University of York regulated Department of Biology Ethics Committee and Edinburgh Zoo, part of the Royal Zoological Society of Scotland (RZSS).

Study site

Research was undertaken at Budongo Trail, Edinburgh Zoo, Scotland. The facility was built in 2008 and has capacity for 40 chimpanzees. The facility is over 1500m^2 and comprises of three indoor 'pods', an off-show bedding area and an outdoor enclosure, all linked by tunnels. Each of the 'pods' and the outdoor area contain large, wooden climbing structures with built in metal baskets that can be used for day beds, encouraging natural bedding behaviours. This layout allows the animals to choose their locations and social proximity to other group members and to split into sub-groups that vary in composition of individuals, allowing their natural fission-fusion social system to be expressed.

Subjects

During the study period there were 18 adult chimpanzees (10 females and eight males; see chapter three). The group comprised of individuals originally either from Edinburgh Zoo or Beekes-Bergen Safari Park who were integrated into the Edinburgh group in 2010 (Schel et al., 2012). Before living in the safari park, these animals were housed in an experimental laboratory. None of the 18 animals had been exposed to music since 2010. Prior to 2010 it is believed that all Edinburgh Zoo individuals heard music played for caretakers but the music exposure history of the Beekes-Bergen individuals was unknown.

Materials

Music was played using an Ipod Nano® and an Anchor Liberty minivox battery powered speaker. Music was played into one target pod through open mesh areas in the keeper's doors at a height of approximately 1.5m. To ensure the majority of the sound was channelled into the chosen pod and that as little noise as possible was heard in other areas of the enclosure, music was broadcast from a speaker housed in an insulated box (see appendix 1). Sound levels were set so that no music could be heard in at least one of the other indoor pods and it was audible at a comfortable level for human experimenters at all points in the target pod. Data were commentated in real time onto an Olympus DM650 dictaphone and transcribed later using Olympus Sonority software.

Stimuli

Since the music history of the chimpanzees is unknown prior to 2010, the songs used for the pop/rock music were those released into the charts from 2010 onwards to ensure they were novel to all animals. Classical instrumental music with between 50 and 90 BPM has been shown to increase social grooming in laboratory chimpanzees (Videan et al., 2007) and was therefore used for this study. Music without dramatic passages were chosen to increase potential for the music to have a calming effect. As most contemporary pop/rock music is much faster than classical music, songs with greater than 90 BPM were chosen to replicate radio music for keepers/care givers use when preparing food, cleaning enclosures etc.

Fifteen pieces of music were selected: seven classical pieces and eight pop/rock songs (see appendix 2). One piece of music followed immediately after the previous one finished. The running time of the classical playlist was 30 minutes and 23 seconds and the pop/rock playlist lasted 30 minutes and 2 seconds. Music was equalised in overall amplitude using Audacity auditory editing software. Each piece of music was brought to an average amplitude by reducing the volume of loud passages and increasing the volume of quieter ones. For each type of music, three playlists were created with each version having a different order. This was done so the chimpanzees did not habituate to the stimuli or display anticipatory avoidance behaviour towards certain songs. For each genre of music the three playlists were played six times with the exception of the first classical and pop/rock lists that were each played seven times.

Data Collection

Data were collected over 14 weeks (April-May; August –September 2013). Four experiments were conducted each week on two separate days between 12:00 - 13:00 and 14:15 – 15:15. In total there were 38 hour-long trials; 19 where music was played into pod two (9x classical music and 10x pop/rock) and 19 where music was played into pod one (10x classical music and 9x pop/rock). The order of music and silence were counterbalanced across trials with music occurring in the first 30 minutes of the trial 19 times.

Instantaneous scan samples (Altmann, 1974) were taken recording the identity and behaviour of each individual present in the target pod (Table 1). During each condition there were 11 scans per condition; 10 with an inter-scan interval of three minutes, and a final scan that occurred two minutes after the tenth scan (see appendix 3). The 13 behaviours recorded during scan samples were collapsed down into five behavioural categories; active, passive, socially active, self-grooming and abnormal (Table 9). In addition to the scan samples, all occurrence data on exits and entrances from the experimental pod were recorded as well as all aggressive events (displaying, chasing and/or hitting another individual) within the target pod.

Table 9 – Behaviours recorded in instantaneous scan samples

Behaviour category	*Behaviour*	*Description*
Passive	Resting	Resting when standing, sitting or lying
Active	Travel	Walking or running
	Climbing	Travelling in an upwards trajectory
	Foraging	Moving whilst looking for food
	Eating	Consuming food
Social Active	Playing	Interacting with another individual or an object in a playful manner
	Grooming another	Manipulating the hair on another's body
	Receiving grooming	Having hair manipulated by another
	Mutual grooming	Two individuals manipulating the hair on the other conspecific's body
Self-grooming	Self-grooming	Manipulating the hair on own body
Abnormal	Abnormal and stress related behaviours	Any abnormal behaviour indicative of stress: regurgitation and reingestion (R/R), urine drinking, faeces eating, plucking fur, scratching and yawning
Not included	Aggression	Displaying, chasing or physical contact in an aggressive manner
	Other	Anything else not mentioned above; exact details noted

<u>Data Analysis</u>

Do the chimpanzees approach or avoid the target pod where music is playing?

The time each individual spent in the music pod for each of the music and silence conditions within a trial was calculated from their entry and exit times. If an individual spent multiple periods in the pod, a mean duration spent in the target pod during each of the silence and music periods was calculated. The minimum requirement for a trial to be included in the analysis for a particular individual was that the individual had to be present for at least three minutes in each of the two (music and silence) conditions. The mean duration each animal spent in the target pod during the silence and music periods from all its eligible trials was then calculated. All individuals were present in at least two eligible trials (range 2-21) resulting in N= 18.

Does BPM of the music affect the chimpanzees' use of space?

To see if the BPM of certain songs across the classical and pop/rock genres had different effects on chimpanzees' use of space, the song playing as an individual entered and/or exited the music pod was identified. The criterion for an individual to contribute data to this analysis was that an individual had to enter and exit the pod at least five times during music periods, resulting in N= 18. The mean BPM from all of an individual's exit or entry songs (see supplementary material) was then calculated.

Does music affect the behaviour of the individuals exposed to the music?

Data from the instantaneous scan samples were used to examine active, passive, socially active, self-grooming and abnormal behaviour in music and silent periods. For each individual we only included data from 'eligible' trials where individuals were present at for at least one scan in each of the music and the silence periods so we could examine differences between these matched periods. This helped to control for inter-day differences in the behaviour of the chimpanzees due to changes in group dynamics or external factors, such as fluctuations in visitor numbers or building maintenance being undertaken.

Separate analyses were run for each of the five behaviour categories (active, passive, socially active, self-grooming and abnormal). Across eligible trials, the number of scans in which an individual demonstrated a behaviour category (e.g. active) was divided by the number of scans he/she was present in that condition (music / silence) to create proportion measures. To enter this analysis an individual's proportions had to be based on data from a minimum of two trials, resulting in N= 18.

The total number of aggressive events where an individual was acting as an aggressor in music and silent periods across trials was divided by the total time that individual was present in the associated condition (taken from entry/exit times). This then gave the rates of aggression per individual per hour in the target pod during music and silence. Only individuals who were observed acting as the aggressor at least once (N= 11) were included in this analysis.

Do Classical music and Pop/rock music have differing effects on the use of space and behaviour of the animals?

To compare the effects of classical and pop/rock music on duration in the music pod, rates of aggression and proportion of scans engaged in active, passive, socially active, self-grooming and abnormal behaviours, difference values (total or mean value from one genre minus the total or mean value from the matched silence periods) were created. The criterion for entry into the "classical difference" and "pop/rock difference" analyses was being present for at least one scan or 3 minutes duration in both the music and silence periods of a single experimental trial, for a minimum of two classical trials and two pop/rock trials, resulting in N= 16 individuals.

Statistical analyses

All tests were two-tailed with alpha level set at 0.05. In conjunction with visualising data on histograms, Shapiro-Wilk tests were run and indicated that all data were normally distributed and thus suitable for parametric tests. Paired T-tests were conducted to test for differences between music and silence conditions and independent T-tests were used to test between "classical difference" and "pop/rock difference" using SPSS v.21. Effect sizes (*d*) were calculated using an online tool (http://www.uccs.edu/~lbecker/), whilst the sample sizes that post-hoc power analyses indicated would be required to reach significance were calculated using G*Power 3.1.9.2. When using Cohen's *d* as an effect size, a large effect would be considered 0.80 and above, a medium sized effect would be 0.50 and 0.20 would be a small effect (Cohen, 1992).

Results

Do the chimpanzees approach or avoid the target pod where music is playing?

The chimpanzees (N= 18) showed no significant difference in the amount of time they spent in the pod when music was playing (mean= 914s, SD 341) compared to when the pod was silent (mean= 975s, SD 191; Paired t-test T(17)= -1.11 p= .280; *d*= 0.22). The effect size of 0.22 was small and post-hoc power analyses indicated that for such a small effect to become significant we would have needed to have tested 225 individuals.

Does BPM of the music affect the chimpanzees' use of space?

The mean BPM of the music playing when the chimpanzees (N= 18) entered the music pod was significantly lower than the BPM of the songs they exited to (Paired t-test T(17)=-2.23, p=.039; *d*= 0.04; Figure 13).

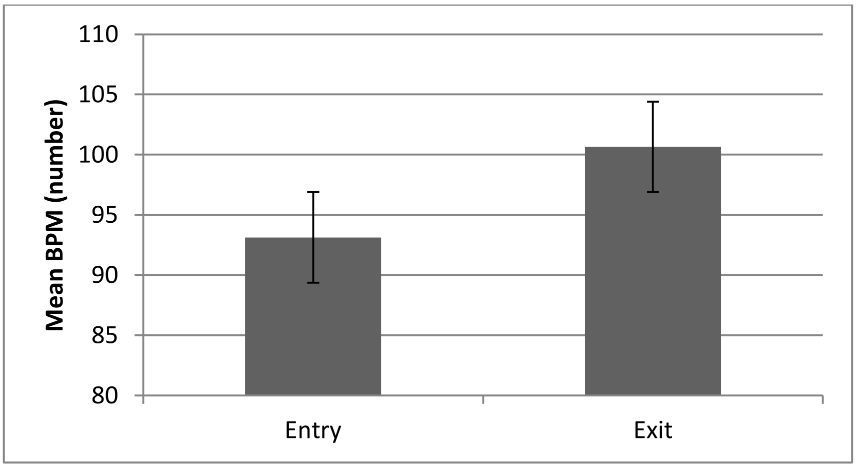

Figure 13 – Mean BPM of songs playing when chimpanzees entered and exited the pod with the music playing. Error bars represent standard error.

Does music affect the behaviour of the individuals exposed to the music?

There was no difference in the proportion of time chimpanzees spent being passive or self-grooming between music and silence conditions but there were trends for chimpanzees showing less abnormal behaviours when the music was playing and more active behaviours during the music. The chimpanzees also displayed significantly fewer socially active behaviours whilst the music was broadcast (table 10).

Table 10 – Results for Paired T-tests comparing mean proportion of scans spent engaging in Passive, Active, Socially Active, Self-grooming and Abnormal Behaviours between Music

and Silence trials. Trends are italicised and significant differences are shown in bold and underlined.

Behaviour	Mean proportion of music scans engaged in the behaviour category (SD)	Mean proportion of silence scans engaged in the behaviour category (SD)	T value (df= 17)	p value	*d*	Sample size power analyses indicated would be required to reach significance
Passive	62.70 (17.50)	63.29 (15.31)	-0.10	.920	0.04	6766
Active	*12.94 (8.44)*	*9.94 (6.63)*	*2.02*	*.059*	*0.28*	*168*
<u>Social Active</u>	**<u>8.00 (7.49)</u>**	**<u>16.33 (10.69)</u>**	**<u>-5.05</u>**	**<u><.001</u>**	**<u>0.91</u>**	**<u>N/A</u>**
Self-grooming	4.83 (4.62)	5.39 (3.90)	-0.73	.477	0.09	1607
Abnormal Behaviours	*0.65 (1.28)*	*1.35 (1.80)*	*-1.88*	*.080*	*0.33*	*122*

Rates of aggression of the chimpanzees (N=11) were not significantly different between when music was playing (mean= 0.78/hr, SD 0.85) and when there was silence (mean= 0.26/hr, SD 0.48; Paired t-test T(10)= 1.72, p= .115; *d*= 0.57).

Do Classical music and Pop/rock music have differing effects on the use of space and behaviour of the animals?

There were no significant differences in the chimpanzees' (N= 16) duration spent in the music pod, the proportion of scans engaged in self-grooming, active, socially active, passive and abnormal behaviours between classical and pop/rock music (table 11) but there was a trend for the chimpanzees showing a higher rate of aggression during music compared to matched silence periods when pop/rock music (Mean= 0.53 SD 1.09) was being played compared to classical (Mean= -0.02 SD 0.62). However, post-hoc Paired T-test found that rates of aggression were not significantly higher during the pop/rock music (Mean= 1.88 SD 4.16) than during the associated silence periods (Mean= 1.06 SD 2.74; Paired t-test T(15)= -1.77, p= .097; Bonferroni corrected alpha value = .025).

Table 11– Results comparing "classical difference" with "pop/rock difference". Positive mean values indicate more of the behaviour was observed in the music period (classical or pop/rock) compared to the matched silence period; whilst negative mean values indicate more of the behaviour was observed in the silence period compared to the matched music period (classical or pop/rock).

Type of Data Analysis	Mean "classical difference" from matched silence periods (SD)	Mean "pop/rock difference" from matched silence periods (SD)	T value (df= 15)	p value	*d*	Sample size power analyses indicated would be required to reach significance
Duration	-31 seconds (148)	5 seconds (193)	-0.54	.598	0.14	665
Passivity	5.08 (19.44)	-5.10 (12.95)	1.55	.143	0.39	88
Activity	1.72 (5.18)	1.28 (5.03)	0.23	.817	0.06	3612
Social Activity	-4.39 (5.12)	-3.94 (5.01)	-0.26	.800	0.06	3612
Self-grooming	-1.00 (3.01)	0.44 (2.83)	-1.26	.225	0.30	147
Abnormal Behaviours	-0.45 (2.03)	-1.20 (3.42)	0.66	.522	0.17	452
Aggression	-0.02/hour (0.64)	0.53/hour (1.12)	-1.68	.113	0.43	73

Discussion

The chimpanzees seemed to show little reaction to music generally. Individuals spent similar amounts of time in the target pod regardless of whether or not music was playing. This suggests that the animals did not actively seek out the music but equally they were not trying to avoid it. I did, however, find that the music the chimpanzees entered the pod to had a significantly lower number of BPM than the music they exited to. This suggests that they may show a 'preference' for music with lower BPM. This supports Videan et al.'s (2007) findings that music with lower BPM had more positive effects on laboratory chimpanzees, in this case in terms of reducing aggression. The stimuli were specifically chosen so that the pop/rock music had higher BPMs than the classical music and I found a trend for more aggressive events during music than silence when the type of music was pop/rock rather than classical, suggesting a possible link between higher BPMs and increased aggression. Interestingly, however, in contrast to my findings Videan et al., (2007) found that vocal rather than instrumental music decreased aggression more. Further research is needed to test whether type of music (vocal / instrumental) or tempo (BPM) has a greater impact on aggression rates in chimpanzees. Manipulation of the tempo of the same pieces of music may be an effective way to further test to effect of tempo on chimpanzees' use of space or behaviour.

When considering both genres of music together, significantly fewer socially active behaviours (playing and grooming) were displayed by the chimpanzees when the music was playing compared to when there was silence. As mentioned above, in these studies I have chosen to consider something as enriching if the target animals display positive welfare changes, such as an increase in social behaviours. The finding that the chimpanzees showed less play and grooming behaviours during the music contrasts with Howell et al. (2003), who found music increased social grooming, and strongly suggests a lack of enriching effect. I also found a trend towards an increase in active behaviours, whereas Howell et al. (2003) found an increase in inactive behaviours. This could suggest that whilst the chimpanzees in our study were not actively trying to avoid the target music pod when the music was playing, it was because the cost of avoiding a preferred pod, being in proximity to a preferred individual etc., may have been too high. Instead they may have tried to find areas within the same pod where they could not hear the music or the volume was not as great, which lead to an increase in their activity.

Additionally, I found a trend towards music reducing abnormal behaviours. Although the effect size is small, similar results were found by Wells et al. (2006). They found a trend towards a reduction in what they termed abnormal behaviours, when a group of gorillas were exposed to classical music. However, the constituent behaviours that made up their category of abnormal behaviours did not include regurgitation and reingestion as in our study. By contrast, Robbins and Margulis (2014) reported that both classical and rock music tended to increase the prevalence of regurgitation and reingestion in their three gorillas, as well as hair plucking and stereotypical locomotion. It is likely that the sampling technique used in our study was not optimal for detecting differences in abnormal behaviours, which can happen very quickly and be quite subtle. I address this possibility in study 2, which aimed to explore the effect of music on abnormal behaviour in more detail.

Study 2: Individual Observations

Aim and research questions

This study aimed to examine the effect of music on rarer, abnormal behaviours that may have been missed in study 1 due to instantaneous scan sampling (Altmann, 1974). In this study I employed continuous focal sampling, which is a more sensitive method for observing abnormal behaviours and meant we were able to calculate exact durations engaged in each type of behaviour.

I aimed to address the following questions: i) Does the presence of music increase or decrease abnormal behaviour rates in focal individuals compared to matched silent periods? Based on the results of study 1, we predicted that music would lead to a decrease in abnormal behaviours and ii) Do classical music and pop/rock music have differing effects on the rate of focal animals' abnormal behaviour?

Methods

Subjects

For this study, I focused on three individuals: Rene, Paul and Lianne. These individuals were chosen as long-term behavioural data (Slocombe, unpublished data) showed that they displayed the highest rates of abnormal behaviours of the 18 chimpanzees, making them ideal candidates in which to examine any effects of music on abnormal behaviours.

Stimuli

The same music and playlists were played into pods one and three simultaneously using two sets of the materials used in Study 1. This was done in order to increase the chances of the focal individual hearing the music, whilst also providing areas without music so that it could be avoided. Data was dictated and transcribed as in Study 1.

Data Collection

Data were collected from January to May 2014. Before undertaking data collection, A Priori power analyses were run, which determined that with a power of 0.8, to obtain an effect size of 0.5 would require 34 trials for each individual. Whilst we conducted 37 trials for Lianne, logistical constraints meant we only ran 26 trials for Rene and 29 for Paul (total 92 trials). The first 30 minutes was a control silence period, followed by 30 minutes of music and then a second 30 minutes of silence. Continuous focal sampling (Altman, 1974) was used for a period of 90 minutes, with the start and end times of each behaviour (table 9) recorded so exact durations could be calculated.

As individuals could choose to avoid the music, in some trials the focal individual was not exposed to music during the music period. I only included data from the trials when the focal individuals were actually exposed to music (present in pod 1 or 3) for at least five minutes during the 30 minute period when music was played. Using this criteria resulted in 12 trials (7 from Paul, 1 from Lianne and 4 from Rene) being removed from the dataset, leaving a total of 80 trials (36 for Lianne and 22 for both Rene and Paul). Of these 80 trials, the type of music played was either pop/rock (37; 12 for Rene, 9 for Paul and 16 for Lianne) or classical (43; 10 trials for Rene, 13 for Paul and 20 for Lianne).

If individuals were observed for much longer in one condition than another, they would have had more opportunity to display a wider variety of behaviour in the condition with more observation time. To counter this potential problem and to ensure that I was comparing similar time periods across music and silent conditions, a random number generator (www.random.org) was used to select which of the two silence periods would be compared to the music period from that trial. Secondly, I then compared the observation time in the matched silence and music periods and found that the mean duration of observation in silence periods fell within 1 SD of the mean duration of observation in the music periods (see appendix 4), and so were comparable.

Data Analysis

Data for each of the three individuals was analysed separately. The duration an individual spent engaged in abnormal behaviours during each condition was divided by the observed duration in that condition (e.g. excluding any out of sight periods; in music periods only time spent in the pods where music was playing so the individual was exposed to music). This resulted in a percentage of available time spent engaged in abnormal behaviours being calculated for each silence and music period. To investigate the effect of the different genres of music on behaviour, I created difference values as used in Study 1 (see Data Analysis).

Statistical analysis

All data met the assumptions of parametric testing so tests were run in line with the analyses run in study one; to compare the effects of music and silence on behaviour, paired T-tests were used and to compare the effects of 'pop/rock difference' with 'classical difference' on behaviour, independent samples T-tests were used.

Results

There were no significant differences found in any of the individuals for any abnormal behaviour between when music was playing and when there was silence or between "classical difference" and "pop/rock difference" (table 12), possibly due to the fact that abnormal behaviours were displayed at low levels for all three individuals (table 13).

Table 12 – Results comparing the percentage time spent displaying abnormal behaviours between Music and Silence using Paired T-tests as well as comparing “classical difference” with “pop/rock difference” with Independent T-tests for Rene (N= 22), Lianne (N= 36) and Paul (N=22).

Individual (N)	Music vs Silence T value (df= 21)	p value	Effect Sizes	Pop/rock Difference vs Classical Difference T value (df= 20)	p value	Effect Sizes
Rene (N=22)	-0.56	.585	0.12	-1.85	.079	0.77
Lianne (N=36)	-0.41	.684	0.10	-1.30	.203	0.18
Paul (N=22)	-0.01	.994	0.001	1.10	.286	0.51

Table 13 - Percentage time spent displaying abnormal behaviours during Music and Silence periods for all three individuals

Individual	Music (SD)	Silence (SD)
Rene	2.57 (5.37)	3.52 (6.38)
Lianne	8.34 (14.32)	10.07 (17.06)
Paul	4.11 (7.88)	4.12 (4.22)

<u>Discussion</u>

The results from study 1 suggested that music might decrease rates of abnormal behaviours, however, the results of study 2 do not support this view. As continuous focal sampling was used in study 2, all instances of abnormal behaviour were recorded rather than just those that occurred at the point of a scan sample. Additionally, I had a larger number of trials than in study 1 and focussed on the three individuals with higher baseline rates of abnormal behaviour than other individuals in the group. This means that I was able to accurately see if music was having a specific effect on abnormal behaviours. As music compared to silence generated no significant effects and small effect sizes, I can be relatively confident that overall music was not having an effect on rates of abnormal behaviours in those most prone to displaying them in this group.

Data have been analysed thoroughly in an attempt to find any effects of music or genre on the individuals' behaviour. Running a large number of statistical tests may have increased chances of finding Type 1 errors but given the lack of significant results this does not affect the interpretation of our data. It is, perhaps a greater concern that the great number of null results may be a result of insufficient statistical power and represent type 2 errors. However, the small effect sizes that accompanied most non-significant results indicates that the music is having minimal effect on behaviour and even with a larger number of trials, I would likely not have found any significant differences.

Overall, this study suggests that both classical and pop/rock music have no positive or negative effect on the behaviour of three chimpanzees with relatively high levels of abnormal behaviours. Both studies 1 and 2 have looked at the effect of passively listening to music and suggest that it has little effect on the behaviour of these chimpanzees. However, in these studies the individuals may have disliked the music, but not wanted to leave an area as they may have been grooming, avoiding other individuals etc., making the cost of avoiding the music relatively high.

Chapter 5: Is Music Enriching for Group-housed Captive Chimpanzees (Pan troglodytes)? – Experimental Investigations

Abstract

The effect of passively listening to music on the behaviour of captive primates has been more extensively studied than how these animals react when given the option of controlling their auditory environment. The few studies which have been conducted so far suggest that primates have a preference for silence over music but so far none have investigated how captive chimpanzees would react when given this option. I report one study with group-housed chimpanzees at the National Centre for Chimpanzee Care and another at Edinburgh Zoo. The two studies used devices that allowed chimpanzees to choose if they wanted to listen to music of various types or silence. Both studies showed that there were no persistent preferences for any type of music or silence. When taken together with the results in chapter 4, my results do not suggest music is enriching for zoo-housed captive chimpanzees, but they also do not suggest that music has a negative effect on welfare.

Introduction

In the previous chapter, I focussed on studies that played music to primates to listen to passively. So far few studies have given animals the option to choose what they want to listen to. McDermott and Hauser (2007) gave marmosets and tamarins *(Callithrix jacchus* and *Saguinus oedipus)* choice over what they could listen to and found they preferred slow tempo lullabies over very fast tempo techno music and preferred silence over the lullabies. Two out of three orangutans (*Pongo pygmaeus*) at Toronto Zoo chose to listen to silence over seven different genres of music, including Tuva throat singing, which was included in the study as it is considered the form of music that most closely resembled orangutan long calls (Ritvo and MacDonald, 2016). Both of these studies show that when primates are provided with the ability to control what they can hear, they choose silence or no music, suggesting that music is not enriching.

The two studies above investigated if music itself is enriching. Another study (Line et al., 1990) examined if being able to control music, as an aspect of the environment, could be an effective form of enrichment as studies have established that having control over some aspect of the environment is positive for captive animals (Sambrook and Buchanan-Smith,1997; see chapter 2 for more details). Line et al., (1990) gave five rhesus macaques

(*Macaca mulatta*) access to an enrichment device with three switches; one turned on 'soft rock' radio music, the second turned it off and the third controlled a feeder. Adding the radio feeder gave the monkeys control over their environment and they were recorded to regularly use it. Rates of self-abuse (e.g. self-biting and hair plucking) were significantly lower whilst using the device and there was also a trend for lower cortisol levels in their blood plasma. The researchers made no distinction between the effects of the feeder and the radio music, instead stating that such a device would be a good form of enrichment for laboratory macaques. The results of this study suggest that primates are willing to use music to exercise control over their environment.

In the next two studies I allowed individuals to operate devices that enabled them to have choice over whether they listened to music or silence, as choosing to press buttons carries a much lower cost than leaving an area. We aimed to see if when given this finer level of control over their auditory environment whether chimpanzees would show a preference for music, or a specific genre of music, over silence. The relatively large zoo sample and the use of similar paradigms across two sites mean this study has the potential to generate representative and generalizable results.

Study 1 : **National Centre for Chimpanzee Care**

Aims and Research Questions

This study aimed to give the chimpanzees low-cost control over their acoustic environment and provide the opportunity for the chimpanzees to show a preference for either Classical music, Pop/rock music or silence? To do this an electronic device was created that the chimpanzees could interact with to change the sounds. To look for preferences I analysed the type and number of buttons selected. I predicted that despite having control over playing music or silence, the chimpanzees would still not show a preference for music over silence or a particular genre of music. I also predicted that if they had no interest in music that the chimpanzees' motivation to change what is playing would decrease over time.

Methods

Ethics Statement

The National Center for Chimpanzee Care is fully accredited by the Association for the Assessment and Accreditation of Laboratory Animal Care-International and approval for this study was gained by Susan Lambeth (who lead data collection) from the Institutional

Animal Care and Use Committee (IACUC approval number: 07-92-03887) of University of Texas MD Anderson Cancer Center.

Study Site

The research was undertaken by Meagan Ahlgren and Amanda Richardson at the National Centre for Chimpanzee Care, Michale E. Keeling Center for Comparative Medicine and Research, Department of Veterinary Sciences, The University of Texas M. D. Anderson Cancer Center in Bastrop, Texas.

Subjects

A total of 38 subjects, accommodated in four groups (C2: N = 12 adults; 4F; 8M; C4: N= 9 adults and 1 non-adult; 5F; 5M; C5: N= 6 adults; 3F; 3M; C8: N= 7 adults and 1 non-adult; 6F; 2M) ranged in ages from four to 45 years (mean age 28 years; see appendix 5). Each group was housed in an enriched outdoor compound with partial visual access of other groups as well as access to indoor dens. Sessions occurred within the indoor area but animals had access to the outside throughout. Music was only broadcast inside and could not be heard outside, ensuring the animals could get away from the music if they wanted to do so.

Apparatus and Procedure

Data were collected during July and August 2006. Sessions lasted one hour and were conducted on Tuesdays and Thursdays, with each group having 16 sessions. The chimpanzees were given a device that could be used to select and listen to classical music, rock music (both different from that used in the studies in chapter 4), African folk music or silence (see appendix 6). The type of sound could be selected by putting a finger in one of four, vertically arranged holes within a box, three of which were connected to three separate CD players and one hole that turned the music off. The insertion of a finger would activate the photoelectric sensors inside each hole that triggered the playing of the associated music CD or silence. If no further selection had been made after two minutes, the device defaulted back to silence. The vertical order of the sounds within the device changed every four sessions so that each music choice occupied all four holes equally. Testing only began when more than half of the individuals had interacted with the device. No food rewards were used for reinforcing interaction with the device. The type of sound playing at the start of each testing session varied so that each sound was used at the beginning of a session four times. Data were recorded on the frequency and type of choices by a computer attached to the device, video recording was used to identify the number of interactions each individual in the group had with the device and this was summarised by an observer after each session. Unfortunately it was not possible for specific choices to be attributed to a specific individual, meaning that all analyses related to the type of sound selected were group based.

Data Analysis

As the position of the four buttons changed after every four sessions and the outcome of each button was not associated with a visual feature such as colour or pattern, the chimpanzees likely needed the first session in each block of four to understand the new contingencies of the buttons and choices in those first sessions may have been based an understanding of the previous set of contingencies. As such, I removed the first session of each set of four from the analyses examining button choice, leaving 12 sessions. All preference analyses were conducted on the group level as we could not match choices with individuals.

Do all chimpanzees across groups have a preference for a specific sound?

For this I ran a Linear Mixed Model (LMM) where the dependent variable was the number of times each button was pressed during each session (log 10 transformed as the original variable was not normally distributed), the independent variable was the sound associated with that button (silence, classical, rock and African folk music) and the random effects were the chimpanzee group (N= 4) and the experiment session number (N= 12). 192 data points came from four groups that each took part in 12 sessions.

Does each group have a preference for a specific sound? Do they prefer silence over music?

To identify if each group had a preference for rock, classical, African folk music or silence I compared the distribution of that group's button presses over the four options with the expected distribution (0.25) using one way Chi squared goodness of fit tests. To see if there was a preference for music over silence I ran binomial tests with an expected frequency of 0.75.

Does the interest in pressing the touchscreen decrease over time?

I conducted a Pearson's correlation to examine the relationship between the session number (N = 16) and the mean number of button presses made by the four groups in each session.

Results

Do all chimpanzees across groups have a preference for a specific sound?

An LMM showed that the number of times each button was pressed during each session could not be explained by the sounds associated with different buttons ($F(3,188) = 2.19$, $p = .090$; figure 14) showing there was no overall preference for a specific sound.

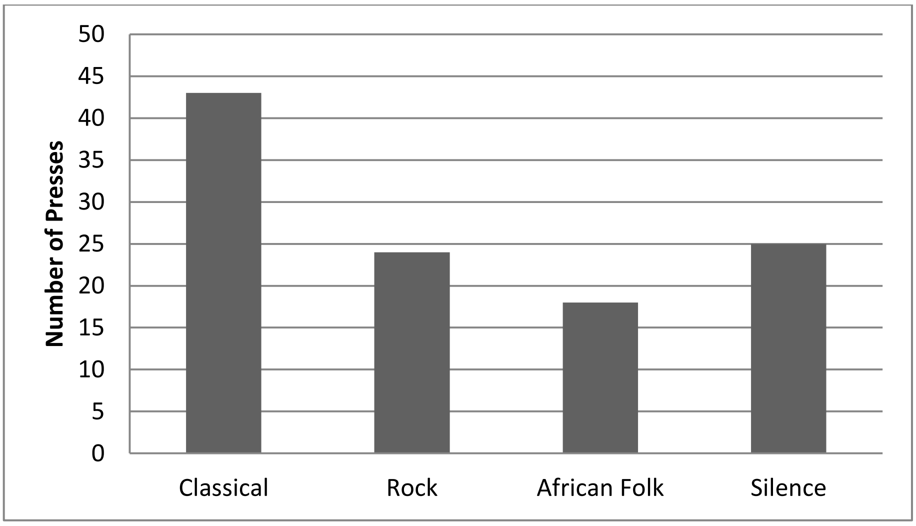

Figure 14 – Choices of the four possible button presses made by the four groups across all 64 trials. Despite the higher number of classical presses, there was no significant difference between the different buttons.

Does each group have a preference for a specific sound? Do they prefer silence over music?

The distribution of Group C2's button presses was significantly different from the expected distribution (table 14), with a preference for classical music (Figure 15). Whether this preference was representative of the 13 individuals in the group, or whether it was driven by a few individuals is unclear. Hannah was responsible for 37% of all of the group's presses (Figure 16), although whether she selected classical consistently is unknown. No other groups' distribution of choices deviated from that expected by chance (Table 14).

Table 14 – Results of tests investigating preferences for each of the four groups. Significant results are in bold.

Group	Chi Squared Goodness of Fit for Button Preference	Binomial (0.75) for Preference of Music or Silence
C2	**X^2 (3)= 11.60, p= .009**	P=. 371
C4	X^2 (3)= 2.88, p= .418	P= .100
C5	X^2 (3)= 5.65, p= .130	P= .358
C8	X^2 (3)= 3.20, p= .326	P= .326

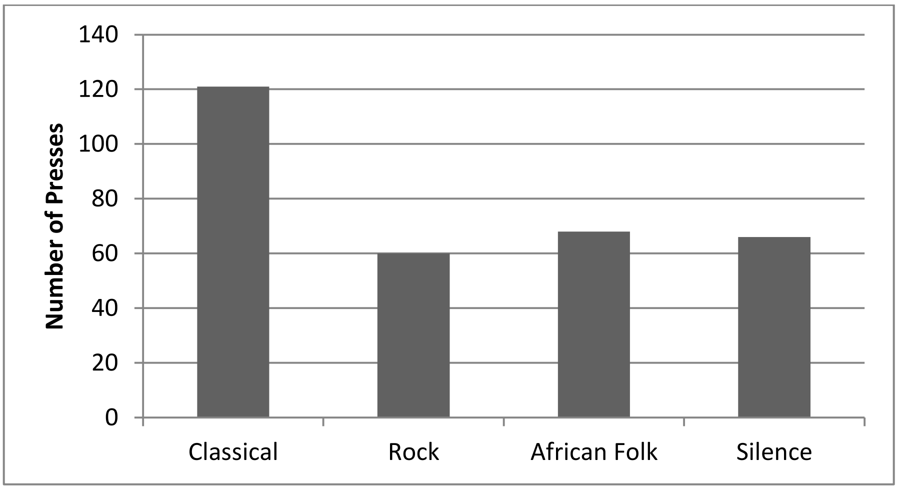

Figure 15 – Choices of the four possible button presses made by group C2

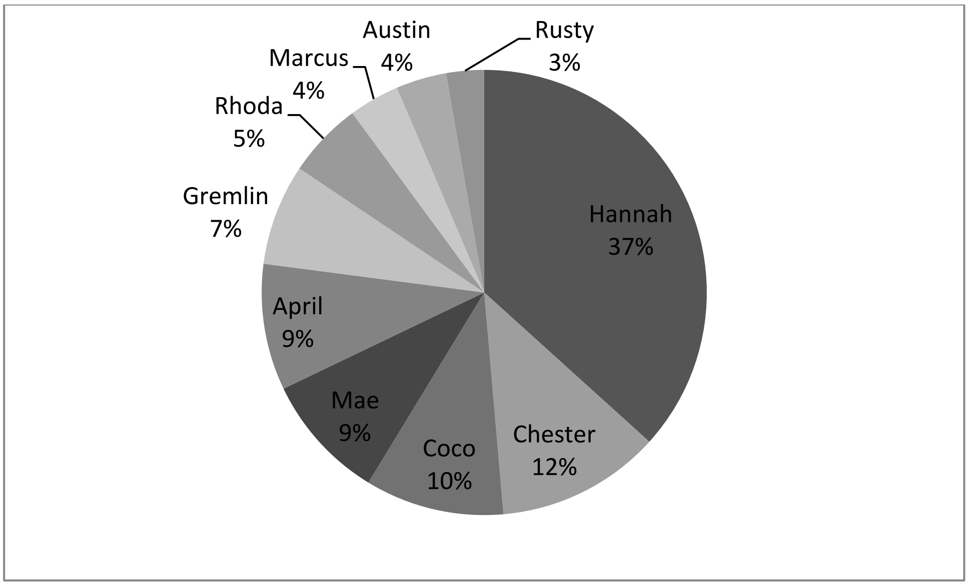

Figure 16 - Percentage of total presses by Group C2 per individual. Pacer, Cordova and Junie are not included in the graph as they did not contribute any button presses.

Does the interest in pressing the touchscreen decrease over time?

A Pearson's correlation (r= -0.55, n=16, p= .026; Figure 17) showed that there was a significant decrease in button presses over time.

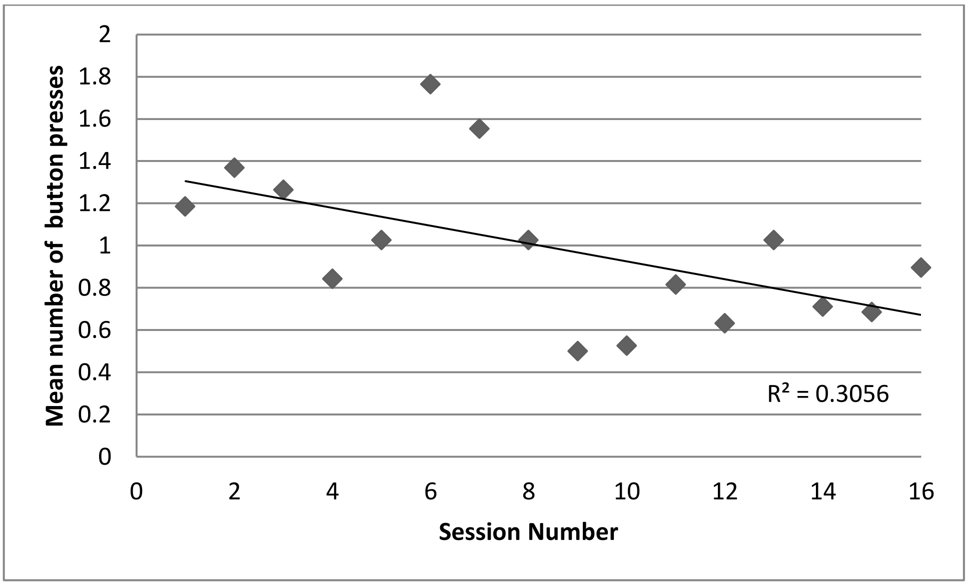

Figure 17 – Scatterplot illustrating the mean button presses across all four groups in each of the 16 sessions with line of best fit.

Discussion

This study shows that, despite having the option to choose the type of sound broadcast and a low cost associated with avoiding a sound they disliked, only one of the four groups (C2) showed a preference for one type of sound, which was classical music and when I looked at all four groups together there was no preference for any of the sounds. The preference of classical music by C2 may not be representative of the whole group as over 75% of button presses were made by just five of the 13 individuals. Recording the type of button pressed by each individual would allow for both group and individual preferences to be established, if they exist.

More strikingly, three of the four groups of chimpanzees did not show not a persistent preference for any of the genres of music or silence. Additionally, all four groups combined showed a decrease in interest in interacting with the touchscreen. These findings may result from an indifference to the presence or type of music in their environment, but they may also result from individuals not understanding the contingencies between the buttons and the resulting sound. They may even have been frustrated by the task, which could explain the decrease in interest. Although testing only began when more than half of the individuals had interacted with the device, this did not mean that those individuals understood the contingencies between certain button choices and the sound that subsequently played. To be able to state with more certainty that the animals were indifferent to the presence or type of music I need to know that they had sufficient opportunity to learn how the device worked.

To address these issues I ran another study at Edinburgh Zoo using a touchscreen device, with a training phase and recorded individual choices.

Study 2: Edinburgh Zoo

Aims and Research Questions

This study aimed to continue the work done in study 1, investigating if when given the choice to control the type of sound a device played whether the chimpanzees would show any consistent preferences for silence or music. To improve upon the previous study, a new device was created that was able to record the choices made by individuals and a training phase was introduced to increase the chances that the chimpanzees understood the outcome of each button press.

This study was conducted in the research pods of Budongo Trail. Several individuals were usually present simultaneously in the research pods. Individuals were trained, using food rewards, to press differently patterned buttons on and use a touchscreen to select classical music, pop/rock music or silence. After training was completed there was a period of individual testing, that used rewards to encourage participation, followed by an unrewarded group testing phase that aimed to establish the inherent interest in changing the sounds the device played and the effect of sound button choices on all individuals within the research pods.

This study allowed me to answer the following questions; i) Do chimpanzees prefer music to silence? If individuals had preferences for silence, classical or pop/rock music I expected them to choose the associated button significantly more than expected by chance in both individual and group testing sessions; ii) Is there a difference in the amount of time each individual was exposed to each sound? Based on the finding of study 1 from chapter 4, that music did not affect the chimpanzees' use of space, I predicted that individuals should be exposed to each sound for similar amounts of time; iii) Does the motivation of the chimpanzees to engage with the touchscreen reduce once food rewards are no longer available? As all previous touchscreen research projects conducted with the Edinburgh chimpanzees have used food rewards during testing and training, I predicted that the chimpanzees would become less motivated to interact with the touchscreen once food rewards had been removed, unless listening to certain sounds was intrinsically rewarding; And iv) Do the button choices of third parties affect how long other individuals choose to spend in the research pods? If choices by third parties had adverse effects on individuals in the area, I expected to find a negative relationship between the number of third party sound changes and duration of time in the research pods.

Methods

Study Site

The training and testing took place in the Research Pods in Budongo Trail covering an area of 26.50m^2. Access in and out of these pods (connected to the indoor pods by tunnels) was unrestricted during all sessions.

Apparatus

Stimuli were presented on a 17 inch ELO IntelliTouch touch panel monitor accessible to chimpanzees through a plexiglass testing window. The touch panel was controlled by a customized PC, running Linux Mint. A Bio-Medica Ltd Universal Feeder and pair of speakers were also attached to the computer, while operation of the apparatus was controlled by keyboard, mouse and an additional monitor, which mirrored what was displayed on the touch panel. All experimental programs were written in Python 3 using Kivy libraries.

Subjects

During the testing phase of the project all 18 adults were given the opportunity to participate. If an individual approached the touchscreen and successfully initiated the training session their progress was recorded. Ten individuals never interacted with the touchscreen. One additional chimpanzee started training but did not complete it. Seven individuals completed training but only six of those took part in individual testing. During group testing, all individuals had access to the research pods and could interact with the touchscreen, regardless of their participation in earlier touchscreen training. Six individuals pressed the buttons on the touchscreen during these group sessions. Of these six, four had completed training as well as taking part in individual testing, one had completed training but not taken part in the individual testing and the final individual had not previously interacted with the touchscreen.

General Procedure

Data were collected between January and April 2015. Experimental sessions were run between 09:00 and 10:00 four days a week.

The experimental task on the touchscreen consisted of a green start stimulus, a blue holding screen and a choice screen. The choice screen consisted of three equally sized monochrome buttons, each of which had a consistent outcome (striped pattern played pop/rock music for 3 sec, zigzag pattern played classical music for 3 sec and spotted pattern gave 3 sec silence; Figure 18a, b and c). During training the buttons were the size of a third of the touchscreen to make it easier for the chimpanzees to press the buttons, meaning that there were three possible positions that they randomly appeared in (Figure 18). During testing, when the three buttons were presented simultaneously, the buttons were smaller to increase the diversity of locations the buttons were presented in and to prevent individuals simply being able to keep their finger in the same place and be rewarded for pressing without looking at the pattern of the button. The positions of the buttons during testing were randomly distributed across nine possible positions in each trial (Figure 19).

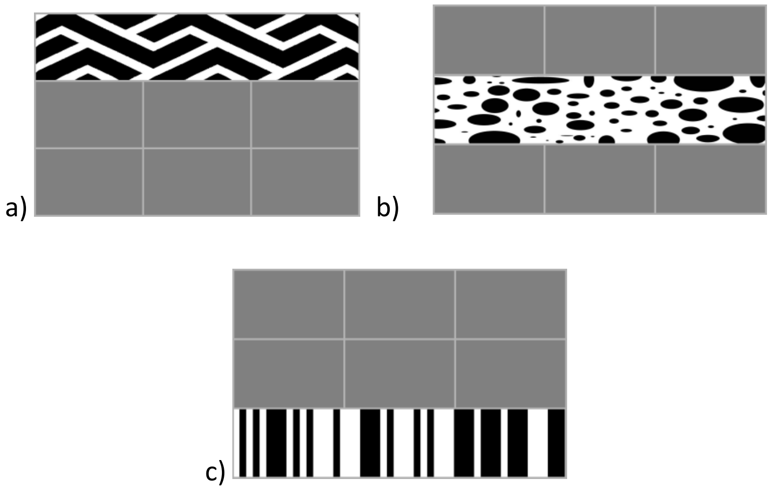

Figure 18 a, b and c – Images of the three touchscreen buttons, as they appeared during training phases. When pressed, each initiated the following actions: (a) turned on classical music for three seconds, (b) turned music off /silence on for three seconds and (c) turned on pop/rock music for three seconds

Training

There were four levels of training that had to be completed before an individual was able to take part in individual testing: 1) the first type of music button (four individuals started with classical first and three with pop/rock first) was presented singly with the first three seconds of a randomly selected piece of music from a playlist of seven playing when the button was pressed, 2) the other music button presented in the same manner as the previous level, 3) the silence button presented singly along with a randomly selected piece of music out of a choice of 14 (7 classical and 7 pop/rock; see appendix 1), which always started at the beginning of the song, so that when the button was pressed the music would stop and there would be silence for three seconds 4) a mixed block with three presentations of each of the three previous levels. Figure 19 shows the order of events within a single training trial and a reward of half a grape was provided when a button was pressed. If an individual did not complete a training level within a single approach of the touchscreen or testing session then the remaining button presses were completed the next time the individual approached the touchscreen, whether it was later in the session or on another day. Once all four levels of training were complete, individual testing could begin.

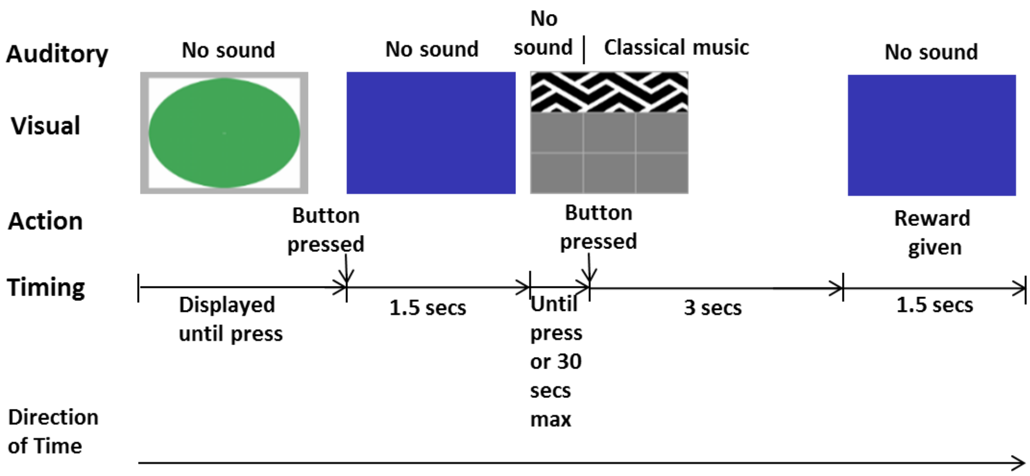

Figure 19 – Illustration of the first trial in a classical button training session, showing the touchscreen images, associated auditory output, actions of the chimpanzees or experimenter, and timings. The downwards arrows indicates a change which is the result of the adjacent action, and is not reflected in an immediate change of visual stimulus. Training continued until the Classical music button had been successfully pressed 10 times, after which the touchscreen was turned off whilst the next training phase was loaded on the computer. If the touchscreen was not interacted with for 30 seconds during a training session, it reverted back to the green circle screen.

Individual Testing

Individual testing began within the group after six individuals had completed at least half of the training stages. Testing trials were broadly similar to training trials (Figure 19), but differed in the following ways: Instead of presenting a large single button, all three buttons were presented at once with their position on the screen randomised over the 9 possible presentation locations (Figure 20). Individuals had to complete 40 trials; 10 where the appearance of the buttons on the screen coincided with classical music starting to play, 10 in which buttons appeared with pop/rock music and 20 where no music accompanied the button screen appearing, the order of which was randomised. Frek was the only individual to complete more than 40 trails as he required two experimental sessions to complete the testing and, due to the randomised order of the trials, he had to complete 68 trials in order to have encountered the required distribution across the three types of trials. The same 14 pieces of music were used for individual and group testing as during training (see appendix 1) and always started at the beginning of the piece of music. If the button screen appeared with music and the button for the same type of music was selected, three seconds of a new randomly selected piece of music from that playlist would play. All button presses were rewarded to ensure non-differential reinforcement for the three buttons.

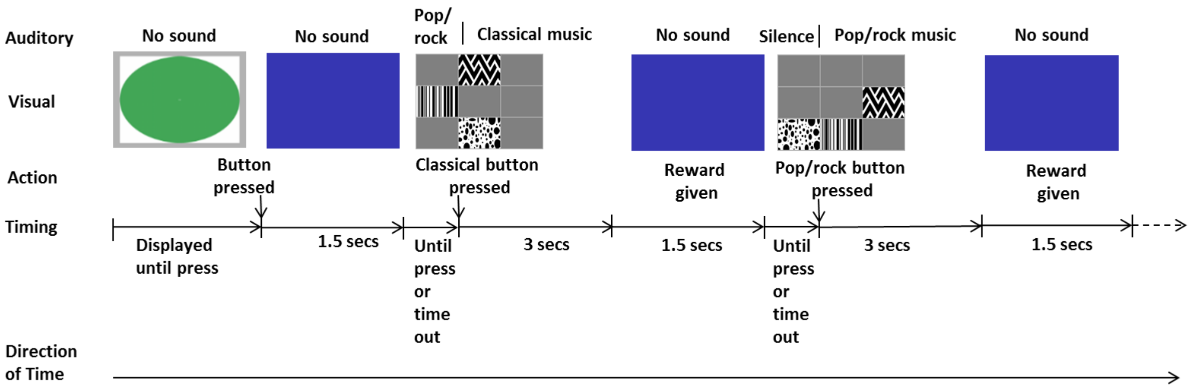

Figure 20 - Example first two trials during a session of individual testing. Layout is as described in Figure 19. Testing continued until 40 buttons, not including the green start button, had been successfully pressed. If the touchscreen was not interacted with for 30 seconds, it reverted back to the green circle screen. If an individual did not complete the testing within a single approach of the touchscreen or experimental session then the remaining button presses were completed the next time the individual approached the touchscreen, whether it was later in the session or on another day.

Group Testing

To encourage the chimpanzees into the research pods a bale of straw (approximately 10kg) and 7kg of primate pellets were spread across the two pods. As the chimpanzees were let into the research pods the touchscreen was already displaying the three buttons in a randomised position. For three trials classical music was already playing as the individuals entered the pods, for three pop/rock music was playing, for three sessions there was silence and for three sessions the touchscreen was not physically available to the participants and no music was played (total of 12 trials). This sound would continue until a button was pressed or the trial ended after 60 minutes. If an individual approached the touchscreen and pressed a button, the corresponding genre of music would play or the music would be turned off, until a new button was pressed. If no new button was pressed that music or silence would continue until the end of the trial. No rewards were given for pressing the touchscreen during this phase. On pressing a button, the buttons would disappear and the selected music or silence would play for 3 seconds. After that, the blue holding screen would be displayed for 1.5 seconds before starting a new trial, which began with the start stimulus. If the touchscreen was silent and the 'off'/silence button was pressed the silence would continue but if one of the types of music was playing and the same button was pressed a new randomly selected piece of music from the same playlist would begin playing. Data was collected on the number and type of buttons pressed by each individual and how long individuals were present in the pod.

Observational Data Collection

Observations were recorded simultaneously by two observers at different vantage points using a Panasonic SDR-S26 video camera and an Olympus DM-650 Dictaphone. The times of all entries into and exits out of the Research Pods were recorded as well as all approaches to the touchscreen. An approach was defined as an individual coming within 20 cm of the touchscreen and staying in front of it for more than five seconds, with their face directed towards the touchscreen. An approach was considered terminated as soon as the individual turned their face away from the touchscreen or started moving away from it. The start and end time of all approaches were recorded, as well as if any buttons were pressed, what type of button was pressed and how many times.

A second coder was used to confirm the start and end time of approaches from video footage. This was used to compare the number of approaches within three randomly selected trials. An Interobserver reliability test was run giving a Kappa value of .959 where $p < .001$, indicating that this behaviour had been reliably recorded.

<u>Data Analysis</u>

In individual and group testing situations, do individuals have a preference for a specific sound? Do they prefer silence over music?

I performed individual level analysis and ran these tests for each of the 6 individuals who completed training and the individual testing. To identify if an individual had a preference for either pop/rock, classical music or silence I compared the distribution of an individual's button presses over the 3 options with the expected distribution (.33) using one way chi squared goodness of fit tests. To see if they had a preference for music over silence I ran binomial tests with an expected frequency of 0.66. For individual testing these tests were run for each of the 6 individuals who completed training and the individual testing (N= 6). For group testing only one individual was included in the analysis for the one way chi squared goodness of fit tests as chi squared tests cannot be run with less than five expected values in each cell. Two individuals were included in the binomial tests as they had more than three button presses.

Is there a difference in the amount of time each individual was exposed to each sound?

For this I ran an LMM where the dependent variable was how long an individual was exposed to each sound during each stay in the research pods, the independent variable was the type of sound (silence, pop/rock, classical), and the random effects were individual identity and the experiment session number. There was a total of 398 data points from 17 individuals that voluntarily entered the research pods during the course of the nine sessions where the touchscreen was active.

Is the duration of time spent in the research pods dependent upon the number of times the sound is changed by third party individuals?

To test this I ran a LMM where the dependent variable was the length of time of each stay in the research pods by an individual, the independent variable was how many times the sound was changed by another individual pressing a button during that stay and the random effects were individual identity and the experiment session number to control for these factors. I only included stays in the research pods where another individual pressed a button or buttons to see the effect of the sound being changed by third party individuals. Data was analysed on 196 pod entries from 17 individuals that voluntarily entered the research pods for a period including at least one button press by a third party during the course of the nine sessions where the touchscreen was active.

Does the interest in approaching or touching the touchscreen decrease over time?

I examined whether interest in the touchscreen, amongst those who chose to approach or interact with it changed with time. For approaches, I calculated the group rate for approaches in each session (total number of approaches by the 12 individuals who had approached the touchscreen at least once divided by the total duration all 12 individuals spent in the pod). I used a Kendall's Tau, due to the small sample size, to see if the rate of approaches changed over the course of the nine sessions where the touchscreen was in use. I then used a Paired T-test to compare the individual rates (N= 12) for the first three sessions with the last three. I then replicated these analyses for button presses, with data being taken from the N=6 individuals who pressed the touchscreen buttons in the group sessions.

Results

In individual and group testing situations, do individuals have a preference for a specific sound? Do they prefer silence over music?

During individual testing, Edith showed a preference for music over silence and pop/rock music over classical music or silence (table 15; figure 21) but did not show any preferences during group testing. Similarly, Pearl showed a preference for pop/rock music over classical music or silence (table 15; figure 22) and no preferences during group testing. Kilimi showed a preference for both pop/rock music and silence over classical music and a trend for a preference for music over silence (table 15; figure 23) but no group testing preferences. Frek showed a preference for music over silence during individual testing (table 15) but did not use the touchscreen during group testing. Eva and Louis (table 15) did not show any preferences. Louis completed training but then did not use the touchscreen during group testing. Cindy completed training but did not participate in individual testing and Emma did not complete training. Although Cindy and Emma did use the touchscreen during the group testing period, they did not have enough presses for statistical analysis to be conducted (Cindy: Silence=2 Class=1 Pop=1; Emma: Silence=1 Class=0 Pop=2).

Table 15 – Results of tests investigating preferences for six individuals. Trends are italicised and significant results are shown in bold.

	Individual Testing		Group Testing	
Individual	Chi Squared Goodness of Fit for Button Preference	Binomial (0.66) for Preference of Music or Silence	Chi Squared Goodness of Fit for Button Preference	Binomial (0.66) for Preference of Music or Silence
Edith	**(X^2 (2) = 8.45, *p* = .015) Preference for pop/rock** **(Silence =6 Class = 13 Pop=21)**	**P= .009 Preference for Music (34/40) over Silence (6/40)**	(X^2 (2) = 0.64, *p* = .727) No Preference (Silence=9 Class=7 Pop=6)	P= .634 No Preference
Eva	(X^2 (2) = 0.96, *p* = .618) No Preference (Silence=19 Class=14 Pop=19)	P= .341 No Preference	N/A (Pop=1)	N/A
Pearl	**(X^2 (2) = 6.65, *p* = .036) Preference for pop/rock** **(Silence=9 Class=10 Pop=21)**	p = .082 No Preference	N/A (Silence=1 Class=1 Pop=1)	N/A
Kilimi	**(X^2 (2) = 9.39, *p* = .009) Preference for silence and pop/rock over classical** **(Silence=18 Class=4 Pop=17)**	*P= .060 Trend for Preference of Music (21/40) over Silence (18/40)*	N/A (Silence=3 Class=3 Pop=5)	P= .227 No Preference
Louis	(X^2 (2) = 1.40, *p* = .497) No Preference (Silence=14 Class=10 Pop=16)	P= .452 No Preference	N/A (Did not participate)	N/A

	Individual Testing		Group Testing	
Individual	Chi Squared Goodness of Fit for Button Preference	Binomial (0.66) for Preference of Music or Silence	Binomial (0.66) for Preference of Music or Silence	
Frek	(X^2 (2) = 3.35, *p* = .187) No Preference (Silence=14 Class= 21 Pop= 27)	**P= .040 Preference for Music (48/62) over Silence (14/62)**	N/A (Did not participate)	N/A

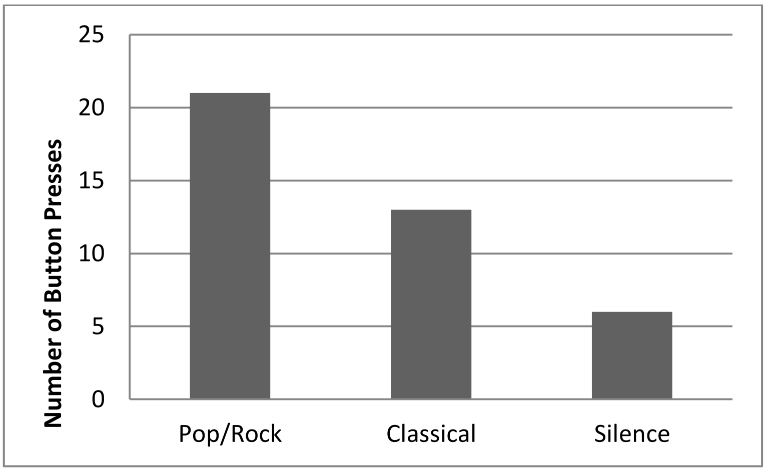

Figure 21 – The number of times Edith pressed each type of button during individual testing

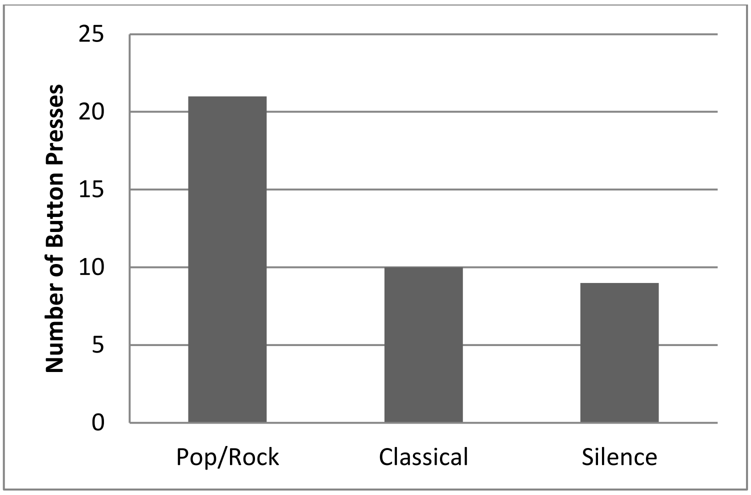

Figure 22 – The number of times Pearl pressed each type of button during individual testing

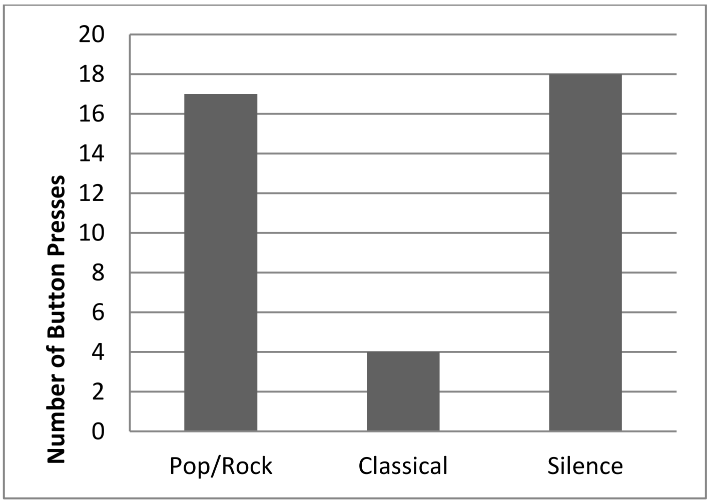

Figure 23 – The number of times Kilimi pressed each type of button during individual testing

Is there a difference in the amount of time each individual was exposed to each sound?

There was no difference in the amount of time individuals were exposed to each of the sounds (F(2,394)=1.05, p=. 352).

Is the duration of time spent in the research pods dependent upon the number of times the sound is changed?

There was a significant effect of the number of times the sound changes on the length of time spent by an individual in the research pods (F(1,193)=89.53 p=<.001, N= 17). Figure 24 shows that as length of time spent in pod increases, so do number of third party presses. If presses by a third party were having a negative effect upon the others in the pod then a negative correlation was expected.

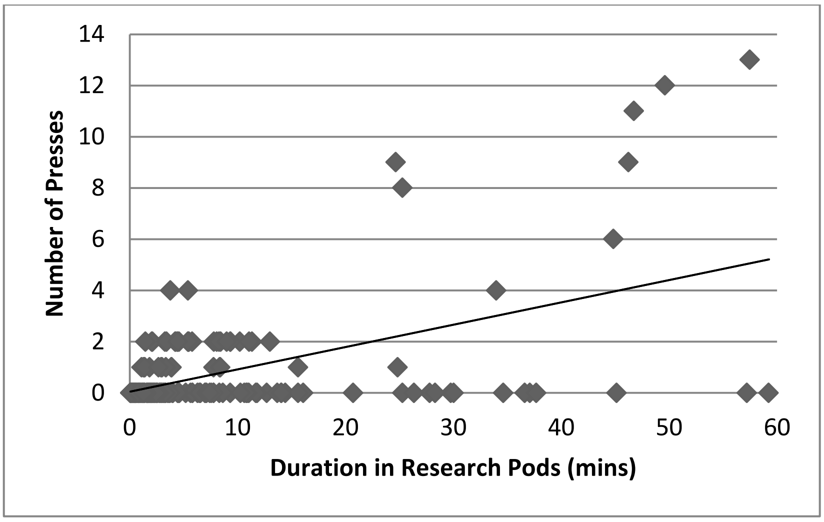

Figure 24 – Scatterplot illustrating relationship between how long the Chimpanzees stayed in the Research Pods and the number of presses by third parties with line of best fit. Each data point represents a distinct stay in the research pods by one of the 17 individuals.

Does the interest in approaching and pressing the touchscreen decrease over time of exposure?

The chimpanzees did not change how often they approached the touchscreen across the nine active sessions (τ_b = 0.23, *n* = 9, *p*= .399) or between the first three and last three sessions (t(9) = -1.09, p= .306). The total number of presses in each session decreased across the nine active sessions, but this association was not significant (τ_b = -0.22, *n* = 9, *p*=.404). Equally when examining the presses of the 6 individuals to interact with the touchscreen during group testing there was no difference in the mean number of presses in the first three and last three sessions (t(6)=-1.07, p= .285). Table 16 shows the number of times each individual pressed buttons during each session.

Table 16 – *The number of times each individual pressed buttons during each of the nine experimental sessions. The total number of button presses across all nine sessions is 45 and it can be seen that, with the exception of the first session, engagement with the touchscreen was low.*

Session Number	1	2	3	5	6	7	9	11	12	Total number of button presses per Individual
Edith	12	0	4	0	0	1	2	3	0	22
Eva	0	0	0	2	0	0	0	0	0	2
Pearl	1	0	1	0	0	0	0	0	1	3
Emma	0	0	0	0	0	1	2	0	0	3
Kilimi	5	0	2	0	2	2	0	0	0	11
Cindy	0	0	0	0	0	4	0	0	0	4
Total number of button presses per session	18	0	7	2	2	6	4	3	1	45

Discussion

This study shows that when the chimpanzees were given the option to learn about the touchscreen device and the outcome of the actions, they did not show any consistent preference for music or silence that lasted over both individual and group trials, which supports the results of study one. The existence of some individual preferences during the individual testing, (e.g. Pearl showed a preference for pop/rock and Frek displayed a preference for music over silence), may have been actual preferences, but as these preferences did not persist into group testing they may have been an artefact of individual reinforcement patterns during individual testing.

Once rewards were removed during group testing, motivation to engage with the touchscreen was low (table 16), particularly after the first session (where rewards were likely expected based on the previous individual testing trials). It is possible that the presses that did occur during group testing were showing genuine preferences, but they occurred at such low levels that we did not have a sufficient number of data points to be able to detect these preferences.

The apparent lack of consistent preferences could also be due to the individuals not understanding the task. Despite having to complete four training phases before individual testing could begin, the animals may not have fully understood the relationship between the visual stimuli (the different buttons) and the auditory stimuli (the different sounds). In particular, even if individuals had a basic understanding of this relationship, the three second exposure to the different sounds after pressing the button may not have been sufficient for them to distinguish between the types of music.

In line with the findings from Study 1 in chapter 4, there was no significant difference in the amount of time the animals were exposed to each sound condition in the group testing sessions. Thus it seems they did not leave the research pods to limit their exposure to any sounds they did not like. I also investigated whether there was a negative relationship between the number of changes to the sounds playing and duration of time spent in the research pods, to check whether exposure to repeated third party sound switches may have had negative effects on group members. I felt it was important to check this, as even if the individuals interacting with the device found it enriching, it was possible this was at the detriment of other group members affected by the broadcast sounds. However, the relationship that was found was positive, meaning that the longer an individual was in the research pods the more times there were changes of sound condition. This shows that having a third party changing between the sounds did not cause them to leave the research pods.

For both studies 1 and 2 I did not test if having control over the environment in the form of manipulating music was an effective form of enrichment. This was decided against as it would have required (i) yoked control trials where the same pattern of music and silence chosen by the chimpanzees in one trial would have had to be played to the animals without them having any control in another trial and (ii) behavioural data on the chimpanzees would have needed to be collected before, during and after access to the touchscreen. Unfortunately it was not feasible to conduct these additional trials and intensive data collection within the time constraints of my PhD and the facilities. Based on the results of Line et al. (1990) it was already known that turning on or off radio music can be an effective form of control over the environment and lead me to feel confident that the chimpanzees in both locations would use the touchscreen to choose what they wanted to hear. As the rates of interaction with the device at the National Centre for Chimpanzee Care were high it is possible that, for these individuals, having control over what they could hear may have affected their behaviour so future studies could be conducted with these animals to establish if engaging with the music device was an effective form of enrichment.

General Discussion

The results of these two studies and the two from chapter 4 show that the presence of music has very limited effects on how chimpanzees use the space within their enclosure or the expression of behaviour and that they do not show a consistent preference for either music or silence. I present convergent evidence from four studies over two research sites that have examined responses of chimpanzees at both group and individual levels to both passive listening and active choice paradigms. This is the first project to include all of these aspects when investigating the effect of music on chimpanzee welfare.

The fact that music had little overall effect on the behaviour of the chimpanzees could have been influenced by relatively low levels of exposure to music over the course of the study. This was an inevitable result of allowing the chimpanzees the option of avoiding the music. During study one, the mean duration spent in the music pod across 18 individuals during each music period was just over 15 minutes and the average total exposure to music across all of the 38 trials that were included in the analyses was 2.77 hours, or just 14.6% of the total time they could have been exposed to music. The results suggest that the chimpanzees were not avoiding the music but equally did not seek it out. If it had been possible to play music for several hours a day, as in other zoo based auditory enrichment studies (Wells et al., 2006; Robbins and Margulis, 2014), there would have been a greater chance of an individual being exposed to the music for longer and more chronic exposure music, may then have had a greater effect on behaviour.

However, another possible explanation for our results could be that chimpanzees do not find music enjoyable. This is strongly suggested by the result from study one in chapter four where the individuals displayed significantly less socially active behaviours whilst the music was playing. Ritvo and MacDonald (2016) found one of three orangutans given the choice of listening to music or silence had no preference for either and that all three animals were unable to distinguish music from samples of scrambled non-music, suggesting that not only is music something primates do not find enriching, it is something they potentially perceive in the same manner as noise.

It is maybe unsurprising that non-human primates do not respond to music positively due to music being a human construct. Music seems to be universal amongst human populations (Cross, 2001) and it is even suggested that human language evolved from vocal origins in the form of communal singing (Dunbar, 2003). However, what constitutes music varies greatly between cultures (Cross, 2001) and therefore it may be unlikely that a human construct with global variation will be considered enjoyable by any other species, even one as closely related as chimpanzees. A recent fMRI study (Norman-Haignere et al., 2015) discovered an area of the human auditory cortex, which is selectively active in response to music rather than speech, regardless of genre, instrumentation or personal enjoyment of the music played. The authors question if this type of organisation is present in the brains of other species or whether this area of selective processing of music is a derived, uniquely human trait. If this is lacking in chimpanzees, and other primates, it could explain why music is something they seem indifferent towards.

In conclusion, unlike previous studies (Howell et al., 2003; Videan et al., 2007) my four studies suggest that it is doubtful that either classical or contemporary pop/rock music have any positive enriching effects for chimpanzees. I suggest that despite the ease and cost efficiency of playing music as a form of enrichment, this is not an effective strategy for group-housed chimpanzees and alternative types of enrichment should be employed. If facilities play music for the enjoyment of the care staff, music with less than 90 BPM should be played preferentially, but as long as the chimpanzees have the opportunity to avoid the music, as they did in these studies, it is unlikely to have any profoundly negative effects on behaviour.

Chapter 6: Are 'Keeper Talks' effective at transmitting educational messages about environmental enrichment within zoos?

Abstract

Modern zoos are concerned with conservation, education and research. In the UK, signage, sessions with school groups and 'keeper talks' are used to educate visitors. However, signs are not always read and education sessions target only a small percentage of visitors. 'Keeper talks' can be viewed by many visitors simultaneously, can increase visitor knowledge and can even create positive attitudes towards animals in visitors. Several studies have investigated their educational value but none have assessed their efficacy for transmitting messages that are counter to popular beliefs. Enrichment research findings do not always match public opinions, with visitors generally preferring natural looking enclosures and activities, even though technology, like touchscreens, can be positive for animal welfare. In the first study I aimed to see if 'Keeper Talks' could educate the public about enrichment in zoos by conducting a questionnaire study of adults visiting chimpanzees at Edinburgh Zoo. I collected data from visitors in three experimental conditions; visitors who heard the standard chimpanzee 'keeper talk', those who heard an extended talk with more enrichment specific information and visitors who did not hear a talk. I used General Linear Models to analyse data from 168 participants. Visitors attending the extended talk had more positive views of touchscreens as enrichment than the other two groups. However, visitors from all three groups believed enrichment should look natural, suggesting that visitors did not learn this general concept from the extended talk. I believe that 'Keeper Talks' can be used to deliver 'new' information but do not seem to be able change previously held beliefs. I also found that very high percentages of visitors answered some of our questions correctly, suggesting that zoo visitors may have higher levels of existing knowledge than predicted, with implications for decisions regarding the level and content of talks. To test this I conducted another study that used questionnaires to assess the perceptions that zoo professionals have about levels of zoo visitor knowledge. Additionally I conducted semi-structured interviews about the aims of 'Keeper Talks' and how their impact is assessed within British Zoos. I found that zoo professionals are mostly under-estimating visitor knowledge and that more time and resources should be allocated for undertaking evaluations into visitor knowledge and the various potential impacts of 'Keeper Talks' that align with the aims zoos want them to fulfil.

Introduction

Modern zoo enclosures aim to reflect the contemporary roles of zoos in conservation, education and research (Kreger et al., 1998). Every year approximately 700 million people, or 10% of the world's population, visit zoos (Gusset and Dick, 2010). Even if this number is an overestimate due to some individuals visiting several zoos or the same zoo multiple times each year (Smith, 2013), zoos have an invaluable opportunity to educate significant numbers of the public. The World Association of Zoos and Aquaria have stated that 'the educational role [of zoos] is to interpret living collections to attract, inspire and enable people from all walks of life to act positively for conservation… and explain human impact on wildlife in both local and global contexts' (WAZA, 2005, p35). This means that zoos need to educate their visitors to understand the issues facing animals in the wild relating to extinction and conservation (Patrick et al., 2013), increase knowledge of the importance of science within zoos (Patrick et al., 2013) as well as the importance of animal welfare and the use of enrichment within zoos (Reade and Waran, 1996).

All zoos in the UK must show evidence of education as part of the licensing process (DEFRA, 2000). There are three main ways of educating the public in UK zoos: informational signage, education sessions with school groups and 'keeper talks', all of which were introduced in chapter one. Static signs in zoos are not read by the majority of zoo visitors (Ross and Gilliespie, 2009) and whilst interactive displays are a more effective educational resource (Bowler, Buchanan-Smith and Whiten, 2012; Whitehouse et al., 2015; Derwin and Piper, 1988; Andersen, 2003) they are not able to answer questions or give visitors tailored information (Knudson et al., 1995; Bright and Pierce, 2002) in the same way that it is possible by speaking to a zoo professional. Educational sessions within zoos for visiting groups of young people are able to educate whilst allowing hands on interaction (Patrick et al., 2013) and create empathy for animals (Sanford, 2014). However, whilst these sessions are beneficial for the individuals who attend, their overall impact is likely to be low due to the relatively few individuals engaging in these sessions. For example, Chester Zoo receives approximately one million visitors annually yet only 30,000 children, just 3% of the overall visitor number, experience an education session (Moss, Esson and Bazley, 2010).

'Keeper Talks' appear to offer solutions to the problems created with signage and education sessions as they can reach a large number of people simultaneously and allow the opportunity for questions and discussion. Such talks have been found to improve visitor enjoyment of an animal enclosure (Mortan, 2001), increase interaction with educational material (Povey and Rios, 2002) as well as aid memory of key messages after as long as six weeks (Heinrich and Birney, 1992).Whilst the benefits of such presentations are numerous, having animals performing in them causes an ethical dilemma (Hosey et al., 2013 p.471). Price et al. (2015) found that whilst zoo visitors who observed either a 'training demonstration' or a 'research demonstration' had a more positive attitude towards apes and greater knowledge than visitors who had not been present at either demonstration, there was no significant difference in attitude or knowledge of visitors between the two types of demonstrations. This suggests that the format and/or content of the talk is not as important as the presence of a knowledgeable member of staff sharing information in a well-structured manner at the same time as some form of active element involving the animals. Talks coinciding with animal feeds, often referred to as 'Keeper Talks', provide an active element to garner the attention of the public whilst avoiding the need for animals to perform. However, these talks require a lot of resources and husbandry must be scheduled to fit around talk schedules. As such, it is vital for each zoo to assess that these talks are actually meeting their educational goals and aim to publish and share their findings (Balmford et al., 2007; RSPCA, 2006). The first step in this process is for zoos to have clear educational goals for their keeper talks. For instance are keeper talks aiming to increase knowledge, consolidate existing knowledge, change attitudes or change behavior?

Previous studies have found that 'Keeper Talks' can be used to successfully convey ideas about conservation that lead to visitor behaviour changes (Heinrich and Birney, 1992; Swanagan 1993, 2000). In addition they have been shown to increase knowledge of research and conservation work done by zoos (Price et al., 2015) and the importance of training programmes for animals within zoos (Anderson et al., 2003). They can also affect how confident visitors feel about responses; Price et al. (2015) found that visitors' ratings on a 1-10 scale in response to the question 'Are you knowledgeable about the zoo's work in research and conservation?' were 18% higher in individuals who attended a demonstration compared to those who did not. These successful studies were however, perhaps consolidating or refreshing existing knowledge in many of their visitors, rather than challenging existing views with new, possibly counter-intuitive messages. However, so far no studies have assessed the ability of these talks to transmit messages about environmental enrichment. Additionally, the above studies were not trying to transmit information that the public could find counter-intuitive. For 'Keeper talks' to be effective within a zoo-educational setting, however, they need to be able to successfully challenge long held beliefs, as there are several areas where common public perceptions are at odds with scientific findings, including in the field of animal welfare and enrichment.

It is vitally important that visitors to zoos are content with the welfare of the animals they see, but their perception of animal well-being may not be in line with the actual welfare of the animals. Seidensticker and Doherty (1996) found that the public believed that animals displaying behaviours seen in the wild was not indicative of good welfare, yet the performances of these behaviours are considered by researchers to be the exact opposite (Hosey and Skyner, 1997). In addition, visitors rated most naturalistic enclosures as having best welfare, yet this may not always be the case (Seidensticker and Doherty, 1996). In the past few years technology, such as touchscreens, has become more commonly used for animal enrichment (Clay et al., 2011) and have been shown to have positive effects on animal welfare (Clark, 2011; Perdue et al., 2012; Whitehouse et al., 2013). The results of Seidensticker and Doherty (1996) suggest that visitors may view technological forms of enrichment as being less beneficial for animals, but this has not been explicitly tested. Music is a form of enrichment that is frequently used for both laboratory and zoo-housed chimpanzees but the research presented in chapters four and five suggests that music is not an effective form of enrichment for chimpanzees, which challenges the beliefs of many zoo professionals who play music for chimpanzees as part of their enrichment programme. It is possible zoo visitors may also incorrectly believe that music is beneficial for chimpanzees. There is often a conflict for zoos to make animal enclosures and the behaviours displayed by the animals desirable for the public whilst also improving animal welfare, and one way to tackle this conflict is to educate the public to align their understanding of animal welfare with recent scientific findings.

The presence of environmental enrichment has been shown to increase visitor dwell time at animal enclosures (Davey, 2006). McPhee at al. (1998) asked zoo visitors if specific enclosures required enrichment and how 'happy' the animals were that lived in those enclosures and results indicated that visitors generally thought enrichment was important. Zoo professionals are often concerned that the public preference for natural enclosures (Seidensticker and Doherty, 1996) will lead them to also prefer natural looking enrichment devices, which results in many zoos having policies stating that only naturalistic enrichment items can be given to animals. However, if 'Keeper talks' could be used to change public preferences for naturalism within zoos, this would greatly increase the forms of enrichment which zoos would be able to put on public display, improving the welfare of the animals as well as potentially lightening the heavy workload of animal keepers.

Study 1: Zoo Visitor Knowledge

Aims and Research Questions

In the first study, I aimed to understand zoo visitor perception of the use of environmental enrichment for chimpanzees, through the use of questionnaires, and examine if these views were influenced by attendance at and content of keeper talks or related to education level, frequency of zoo visits, and prior understanding of chimpanzee behaviour and cognition. To my knowledge, this is the first study to examine whether 'Keeper talks' can be used to educate the public about enrichment, including non-naturalistic forms of enrichment. In order to do this three experimental conditions were created; visitors who had heard the standard chimpanzee keeper talk, those who had heard the extended talk and visitors who had not heard the talk.

This allowed me to address the questions; do individuals who are presented with relevant information during a 'Keeper Talk' perform better on questions relating to the content than individuals who have not heard that information? And do visitors who believe that humans and chimpanzees are similar believe that music is a good form of enrichment? Based on my personal conversations with zoo visitors, many have expressed surprise that research is suggesting music is not an effective form of enrichment for chimpanzees, based on the visitors' knowledge of the similarities between humans and chimpanzees. I therefore predicted that participants who believed the two species to be similar would believe that music is an effective form of enrichment.

Methods

Ethics Statement

Visitor participation in the study was completely voluntary. Consent sheets were provided to obtain written consent and participants were given a debrief sheet after completing the questionnaire. The procedure was approved by the University of York Department of Psychology Ethics Committee and Edinburgh Zoo.

Study Site

The study was undertaken at Budongo Trail Chimpanzee enclosure, Edinburgh Zoo, Scotland. The facility was built in 2008 and can house up to 40 chimpanzees. The facility is over 1500m^2 and comprised of three 'pods', a bedding area and an outdoor enclosure, all linked by tunnels. Edinburgh Zoo receives approximately 800,000 visitors each year (Whitehouse et al., 2014).

Chimpanzee Keeper Talk

A talk was given daily at 11:45 by a member of the Presentations department and a chimpanzee keeper. On days when there were 20 or fewer visitors for the talk, it took place on a balcony in Budongo Trail, looking over the outdoor enclosure. On days with greater than 20 visitors, the location moved to the top wall of the outdoor enclosure. During the talk the chimpanzees were given a scatter feed into the outside enclosure to encourage them to be visible during the talk. The standard talk lasted approximately seven minutes and contained the following information:

- Individual identities of the chimpanzees within the group
- Their diet
- How chimpanzees communicate
- Why female chimpanzees have oestrus swellings
- The design of Budongo Trail
- How the enclosure is linked to a conservation project at the Budongo Field Station, Uganda

The exact content of the standard talk varied depending on which member of the presentations department was delivering the talk, as there was no exact script. However, all members of staff were told not to cover any of the areas mentioned in the extended talk.

I gave the extended talk after the standard talk had finished on alternate weeks (table 17). It was approximately an additional three minutes in length. It contained information on:

- The importance of enrichment
- That enrichment does not have to look natural to promote natural behaviours
- That cognitive testing using touchscreens can be an effective form of enrichment
- That music does not seem to be an effective form of enrichment for chimpanzees

For an example full transcript of the extended talk, see appendix 7.

Table 17 - The first date of the weeks when the two talk conditions were delivered.

Standard Talk	Standard plus Extended Talk
26th January	2nd February
9th February	16th February
23rd February	2nd March
9th March	16th March
23rd March	
7th April	

Participants

Questionnaires were collected from January to April 2015. 231 participants were recruited from the visitors within Budongo Trail (Table 18). The participants in the no talk group were recruited after 12:30 in the upstairs area of Budongo Trail, if they could confirm they had not attended any keeper talk at the zoo nor planned to during the rest of their visit. Participants who had heard either the standard or extended talk were approached directly after the talk.

Table 18 – Number of Participants from each of the three experimental groups, the highest level of education each participant completed and the number of participants in the two age categories

Experimental Group	Standard Keeper Talk	Extended Keeper Talk	No Talk
Number of Participants (%)	88 (38)	88 (38)	55(24)
Education Level			
Not completed Primary	2 (2)	3 (3)	1 (2)
Primary	4 (5)	5 (6)	2 (4)
GCSE	14 (15)	5 (6)	7 (13)
A-level	20 (23)	21 (24)	13 (24)
Degree	29 (33)	32 (36)	21 (38)
Postgrad	15 (17)	19 (22)	8 (15)
Age			
6-21	22 (25)	20 (23)	12 (22)
22+	65 (75)	68 (77)	43 (78)

Questionnaire

Participants were given a 15-item questionnaire (see appendix 8) where 12 questions used a seven point Likert scale with anchors that were relevant to the questions that were asked e.g. 1 , Not at all to 7, Extremely. For some questions they were phrased so that the correct answers would be towards the lower end of the scale and for some the answers would be at the higher end. Also, one question used a Likert scale with reversed anchors where 1 was Extremely and 7 was Not at all. These measures were used to avoid participants selecting the same score for each response without fulling reading the questions. Another question gave a forced choice between two options based on knowledge of human and chimpanzee DNA. Two final questions gave five options of demographic information. The topics of the questionnaire included:

- Topics relating to participant knowledge
    - Participants' views on desirable qualities in the environment of a captive animal
    - Participants' view on whether different items/actions were suitable enrichment for chimpanzees

- Knowledge of how genetically similar humans and chimpanzees are
- How similar participants perceive themselves and chimpanzees to be
- Topics relating to participant background
  - Participants' completed education level
  - Frequency of zoo visits

Data Analysis

For analyses we separated all participants into two groups; young people between 6 and 21 years of age (N= 63) and adults over 21 years age (N=168). This was done as only adults over the age of 21 would have sufficient time to complete the majority of levels of education that we looked at. I ran chi-squared goodness of fit tests to ascertain if the distribution of adults with specific levels of educational achievement was equal over the three experimental groups (standard talk, extended talk and no talk group). I found there were no significant differences between the groups, meaning educational level was not confounded with experimental group (Table 18; Table 19).

Table 19 – Results of Chi-Squared goodness of fit tests run to establish if there were significant differences in the number of adults over the age of 21 from each of the three experimental groups across each education level.

Highest Education Level Completed	Chi Squared value (df = 2)	p Value
GCSE (N = 25)	4.16	.125
A-Level (N = 54)	2.11	.348
Degree (N = 84)	2.21	.331
Postgraduate (N = 42)	4.43	.109

Raw data were collected as continuous data but examination of the data through Q-Q plots and the acquisition of significant Shapiro-Wilk tests of normality indicated that the continuous Likert scale measures were not normally distributed. Attempts were made to transform the data but failed to produce normal distributions, due to the high frequency of scores at the extremes of our scales. Therefore, the variables were converted into categorical variables of two kinds. First, for some questions the seven point Likert scales were broken down into two levels; correct (e.g. 5,6,7) and not correct answers (1,2,3 and 4). Second, for questions where the majority of adult participants gave a correct answer, we examined confidence within the correct responses by comparing the maximally confident response (e.g. 7) with the other less confident responses (e.g. 5,6).

For two of the analyses on adults' data the experimental group categories were collapsed into just two categories: extended and standard talks vs no talks. This was done as the information tested by two questions was covered in the standard talk and therefore heard by participants in both the standard and extended talk groups.

I chose to examine two interactions in the adults' data: experimental group with education level and experimental group with frequency of zoo visits. Whilst it would have been ideal to assess all possible interactions, in order to reduce model complexity and increase model stability and power, I chose to focus on these two as they may be important when designing keeper talks and tailoring them to specific target audiences. The experimental group*educational level interaction assessed whether participants who had completed certain education levels gained more from attending either type of 'Keeper Talk' than those with other education levels. The experimental group*frequency of zoo visits interaction assessed whether frequent rather than infrequent zoo visitors gained more from attending a particular type of talk. With the young peoples' analyses the only interaction included was experimental group * age (continuous measure). With the smaller sample size for this age group, the model would have been unstable with more than one interaction term, so I focussed on age as zoo education departments often target resources and sessions to children of particular age groups. The questions that tested information included in talks were subjected to inferential statistics, in order to assess the efficacy of talks in transmitting new information to zoo visitors (see table 20), however, not all questions could be tested due to several having insufficient variation to enter into inferential analyses due to either floor or ceiling effects.

Table 20 – Questions that were included in data analysis

DV	DV measure (type: levels)	IV One (type of variable; Levels)	IV Two (type of variable; Levels)	IV Three (type of variable; Levels)	IV Four (type of variable; Levels)	Interaction One	Interaction Two	N
ADULTS' DATA								
Are Touchscreen an effective form of enrichment? (Score)	Categorical: correct; not correct derived from likert scale (1-4 = not correct' 5-7 = correct)	Experimental Group (categorical; extended talk, standard talk and no talk)	Frequency of zoo visits (categorical; rare (1/year); frequent (2+/year)	Completed education level (categorical: secondary; tertiary)	N/A	Experimental Group* Education Level	Experimental Group* Frequency of zoo visits	168
Is Music an effective form of enrichment? (Score)	Categorical: correct; not correct derived from likert scale (1-3 = correct' 4-7 = not correct)	Experimental Group (categorical; extended talk, standard talk and no talk)	Score for how similar are the mind and behaviour of humans and chimpanzees (categorical: ; Similar(1 to 3 on Likert scale); not similar (4 to 7 on Likert scale)	Frequency of zoo visits (categorical; rare (1/year); frequent (2+/year)	Completed education level (categorical: secondary; tertiary)	Experimental Group* Education Level	Experimental Group* Frequency of zoo visits	168

DV	DV measure (type: levels)	IV One (type of variable; Levels)	IV Two (type of variable; Levels)	IV Three (type of variable; Levels)	IV Four (type of variable; Levels)	Interaction One	Interaction Two	N
Does enrichment have to be similar to something a Chimpanzee may encounter in the wild to be effective? (Score)	Categorical: correct; not correct derived from likert scale (1-3 = correct' 4-7 = not correct)	Experimental Group (categorical; extended talk, standard talk and no talk)	Frequency of zoo visits (categorical; rare (1/year); frequent (2+/year)	Completed education level (categorical: secondary; tertiary)	N/A	Completed Experimental Group* Education Level	Experimental Group* Frequency of zoo visits	167
How confident are participants about the importance of captive conditions engaging chimpanzees in activities that allow them to think? (Score)	Categorical: Maximally confident (Likert scale 7); Less confident (Likert scale 5 and 6)	Experimental Group (categorical; talks and no talk)	Frequency of zoo visits (categorical; rare (1/year); frequent (2+/year)	Completed education level (categorical: secondary; tertiary)	N/A	Completed Experimental Group* Education Level	Experimental Group* Frequency of zoo visits	167

DV	DV measure (type: levels)	IV One (type of variable; Levels)	IV Two (type of variable; Levels)	IV Three (type of variable; Levels)	IV Four (type of variable; Levels)	Interaction One	Interaction Two	N
How confident are participants about the importance of captive conditions allowing chimpanzees to express natural behaviours? (Score)	Categorical: Maximally confident (Likert scale 7); Less confident (Likert scale 5 and 6)	Experimental Group (categorical; talks and no talk)	Frequency of zoo visits (categorical; rare (1/year); frequent (2+/year)	Completed education level (categorical: secondary; tertiary)	N/A	Completed Experimenta l Group* Education Level	Experimental Group* Frequency of zoo visits	168
YOUNG PEOPLES' DATA								
Are Touchscreen an effective form of enrichment? (Score)	Categorical: correct; not correct derived from likert scale (1-4 = not correct' 4-7 = correct)	Experimental Group (categorical; extended talk, standard talk and no talk)	Age (continuous: 6 to 21)	N/A	N/A	Experimenta l Group* Age	N/A	63

DV	DV measure (type: levels)	IV One (type of variable; Levels)	IV Two (type of variable; Levels)	IV Three (type of variable; Levels)	IV Four (type of variable; Levels)	Interaction One	Interaction Two	N
Is Music an effective form of enrichment? (Score)	Categorical: correct; not correct derived from likert scale (1-3 = correct' 4-7 = not correct)	Experimental Group (categorical; extended talk, standard talk and no talk)	Age (continuous: 6 to 21)	N/A	N/A	Experimenta l Group* Age	N/A	63
Does enrichment have to be similar to something a Chimpanzee may encounter in the wild to be effective? (Score)	Categorical: correct; not correct derived from likert scale (1-3 = correct' 4-7 = not correct)	Experimental Group (categorical; extended talk, standard talk and no talk)	Age (continuous: 6 to 21)	N/A	N/A	Experimenta l Group* Age	N/A	63

Statistical Analysis

General Linear Models (GLMs) with a binomial error structure and a logit link were used to investigate the influence of categorical explanatory variables on whether or not the participants gave the correct answer or were maximally confident in their correct response (table 20) . Interactions, as described in the data analysis section, were included in the models to investigate the most relevant interactions between fixed factors. Full models were reported. If a factor that explained significant variation in dependent variable contained three levels, post hoc 2-tailed Fisher's Exact tests were run to establish between which levels the significance differences occurred. All tests were run using SPSS v.21 with an alpha value of p= .05 and Bonferroni corrected to p= .017 for post hoc tests where 3 additional comparisons were made.

<u>Results</u>

The percentages of young people and adult participants, as well as the adult participants that were in the standard, extended and no talk experimental groups who gave correct answers are shown in table 21.

Table 21 – The percentages of adult and young participants that gave correct answers for each question. Young people and Adult data was then split into the three experimental groups. Data from questions indicated with a (*) had insufficient variation to enter into inferential analyses due to either floor or ceiling effects. Those with a (#) were designed to test existing visitor knowledge but they were not entered into inferential analyses as the information tested was not included in either the standard or extended 'Keeper Talk' so did not contribute to assessing the efficacy of 'Keeper Talks'.

Knowledge Tested	% correct answers from Adults (N= 168)	% correct answers from Adults in each group			% correct answers from Young People (N= 63)	% correct answers from Young People in each group		
		No Talk (N=41)	Standard Talk (N=62)	Extended Talk (N= 64)		No Talk (N=13)	Standard Talk (N=25)	Extended Talk (N= 23)
Are Touchscreen an effective form of enrichment?	55.0%	29.2%	46.8%	78.5%	56.6%	41.7%	42.9%	80.0%
Is Music an effective form of enrichment?	38.0%	41.0%	35.0%	42.0%	35.8%	25.0%	42.9%	35.0%
Does enrichment have to be similar to something a Chimpanzee may encounter in the wild to be effective?	6.6%	4.9%	4.8%	9.4%	11.8%	8.3%	23.8%	25.0%
How important is that captive conditions engage chimpanzees in activities that allow them to think?	96.0%	90.2%	96.8%	98.4%	94.3%	100.0%	85.7%	100.0%
How important is it to ensure that the animals are allowed to express natural behaviours?	84.2%	92.7%	98.4%	100.0%	100.0%	100.0%	100.0%	100.0%

Knowledge Tested	% correct answers from Adults (N= 168)	% correct answers from Adults in each group			% correct answers from Young People (N= 63)	% correct answers from Young People in each group		
		No Talk (N=41)	Standard Talk (N=62)	Extended Talk (N= 64)		No Talk (N=13)	Standard Talk (N=25)	Extended Talk (N= 23)
Do humans and chimps share more or less than 90% of our DNA? (#)	87.0%	78.0%	88.7%	92.2%	87.0%	91.7%	76.2%	95.0%
Is knocking on windows is not good form of enrichment? (*)	97%	92.5%	100%	96.9%	96.2%	100.0%	95.2%	95.0%
How important is it to make the enclosure look as similar to the animal's natural habitat as possible? (*)	3.6%	4.9%	1.6%	4.7%	1.9%	0.0%	4.8%	0.0%
How similar do you think the mind and behaviour of humans and chimpanzees are? (#)	43.0%	26.8%	48.4%	48.4%	30.2%	33.3%	33.3%	30.0%
How important is it to ensure that the animals are always visible to visitors? (#)	67.0%	65.9%	62.9%	71.9%	61.1%	58.3%	61.9%	60.0%

Factors predicting adults' responses to question 'Are touchscreens an effective form of enrichment for Chimpanzees?'

Experimental group and frequency of zoo visits explained a significant amount of variation in participant knowledge that touchscreens are an effective form of enrichment but no other main effects of interactions were significant (Table 22) Post hoc 2-tailed Fisher's Exact tests showed a significantly higher proportion of participants gave the correct answer to the question when they had attended the extended talk (51/65) than if they had attended the standard talk (29/62; p= <.001) or if they did not attend any talks (12/41; p= <.001; Figure 25). However, there was no significant difference in the proportion of participants who answered correctly between those who attended the standard talk (29/62) and those who did not attend any talks (12/41; p= .100; Figure 25). Individuals who visited zoos frequently were more likely than infrequent zoo visitors to answer this question correctly (Figure 26).

Table 22 – Results of GLM investigating the relationships between participant knowledge that touchscreens are an effective form of enrichment and potential explanatory variables (Independent variables). Significant variables shown in bold.

Independent Variable	F value (dfs)	p Value
Full model	**(8, 159) = 3.77**	**<.001**
Experimental Group	**(2, 159) = 8.93**	**<.001**
Frequency of Zoo Visits	**(1, 159) = 9.89**	**.002**
Education*Group	(3, 159) = 0.85	.470
Group*Visits	(2, 159) = 1.18	.309

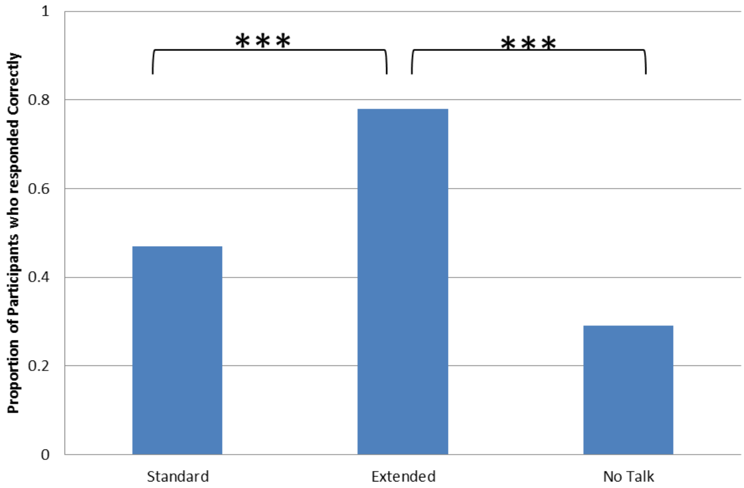

Figure 25 - Proportion of Participants in each of the experimental groups that gave the correct answer to the question concerning whether touchscreens are an effective form of enrichment. ***P <.001

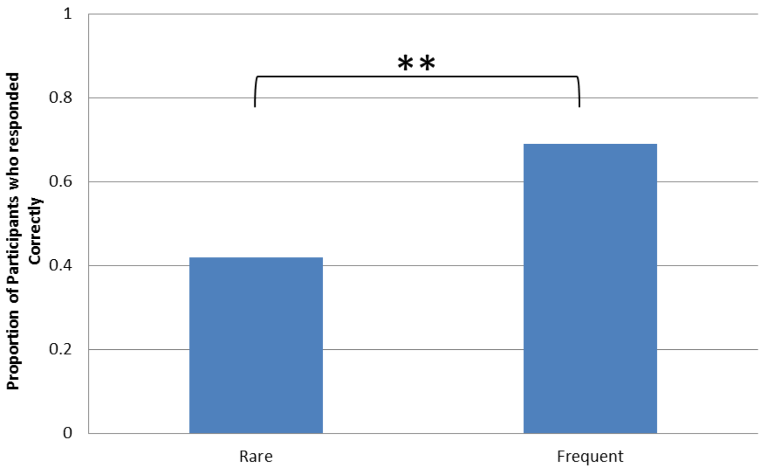

Figure 26 - Proportion of Participants who visit zoos rarely or frequently that gave the correct answer for are touchscreens an effective form of enrichment. **P <.010

Factors predicting young peoples' responses to question 'Are touchscreens an effective form of enrichment for Chimpanzees?'

The age of the participants explained a significant amount of variation in participant knowledge that touchscreens are an effective form of enrichment but no other main effects of interactions were significant (Table 23). Post-hoc Independent T-test found that the age of participants who got the answer correct (mean= 17.42, SD 4.06) was significantly higher than the age of participants who did not get the answer correct (mean= 14.87 SD 5.02; T(52)= 2.06 p= .044).

Table23 - Results of GLM investigating the relationships between participant knowledge that touchscreens are an effective form of enrichment and potential explanatory variables (Independent variables). Significant variables shown in bold.

Independent Variable	F value (dfs)	p Value
Full model	(5, 47) = 1.58	.185
Experimental Group	(2, 47) = 0.67	.518
Age	**(1, 47) = 4.84**	**.033**
Group*Age	(2, 47) = 0.35	.703

Factors predicting adults' responses to 'Is music an effective form of enrichment for Chimpanzees?'

Perceived similarity between chimpanzees and humans explained a significant amount of variation in knowledge that music is not an effective form of enrichment for chimpanzees but no other main effects of interactions were significant (Table 24). Figure 27 shows that a significantly higher proportion of participants who believed humans and chimpanzees were similar gave correct ratings than those who viewed humans and chimpanzees as less similar.

Table 24 – Results of GLM investigating the relationship between participant knowledge that music is not an effective form of enrichment and potential explanatory variables (Independent variables). Significant variables shown in bold.

Independent Variable	F value (df)	p Value
Full model	(10, 156) = 1.34	.212
Experimental Group	(2, 156) = 1.37	.256
Frequency of Zoo Visits	(1, 156) = 0.06	.806
Similarity between humans and chimpanzees	**(1, 156) = 9.42**	**.003**
Education*Group	(2, 156) = 1.51	.225
Group*Visits	(1, 156) = 0.19	.828
Education*Similarity	(1, 156)= 1.62	.204

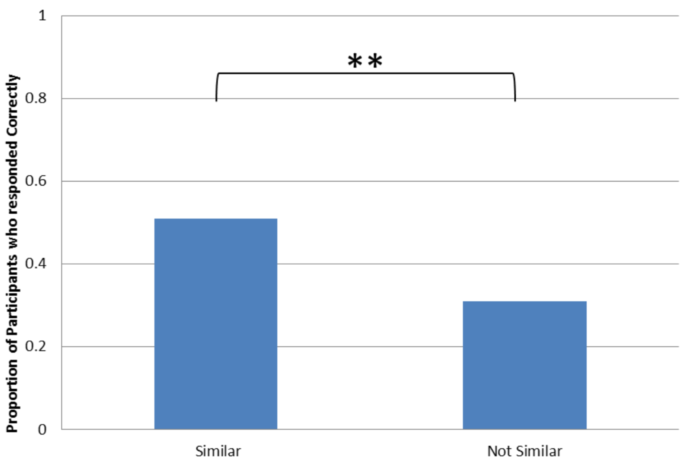

Figure 27 - Proportion of Participants who view humans and chimpanzees as similar or not similar that gave the correct answer for is music an effective form of enrichment. ** P<.010

Factors predicting young peoples' responses to 'Is music an effective form of enrichment for Chimpanzees?'

None of the factors explained a significant amount of variation in participant knowledge that music is not an effective form of enrichment for chimpanzees (table 25).

Table 25 – Results of GLM investigating the relationship between participant knowledge that music is not an effective form of enrichment and potential explanatory variables (Independent variables).

Independent Variable	F value (dfs)	p Value
Full model	(5, 47) = 0.70	.626
Experimental Group	(2, 47) = 0.01	.990
Age	(1, 47) = 2.71	.107
Group*Age	(2, 47) = 0.06	.941

Factors predicting adults' responses to 'Does enrichment have to be similar to something a Chimpanzee may encounter in the wild to be effective?'

None of the factors explained a significant amount of variation in participant knowledge that enrichment does not have to be similar to the wild (Table 26).

Table 26 – Results of GLM investigating the relationship between participant knowledge that enrichment does not have to be similar to something a chimpanzee may encounter in the wild to be effective and potential explanatory variables (Independent variables).

Independent Variable	F value (df)	p Value
Full model	(8, 3) = 0.61	.736
Experimental Group	(2, 3) = 0.01	.986
Frequency of Zoo Visits	(1, 3) = 0.47	.543
Education*Group	(3, 3) = 0.50	.709
Group*Visits	(2, 3) = 0.70	.564

Factors predicting young peoples' responses to 'Does enrichment have to be similar to something a Chimpanzee may encounter in the wild to be effective?'

None of the factors explained a significant amount of variation in participant knowledge that enrichment does not have to be similar to something a Chimpanzee may encounter in the wild to be effective (Table 27).

Table 27 – Results of GLM investigating the relationship between participant knowledge that enrichment does not have to be similar to something a chimpanzee may encounter in the wild to be effective and potential explanatory variables (Independent variables).

Independent Variable	F value (dfs)	p Value
Full model	(3, 47) = 1.12	.351
Experimental Group	(1, 47) = 0.70	.406
Age	(1, 47) = 0.001	.991
Group*Age	(1, 47) = 0.74	.396

Factors predicting adults' confidence level of responses to 'How important is it that captive conditions allow chimpanzees to express natural behaviours?'

Experimental group explained a significant amount of variation in participant confidence of how important it is that captive conditions allow chimpanzees to express natural behaviours but no other main effects of interactions were significant (Table 28). Figure 28 shows that a significantly higher proportion of participants who heard a talk gave the maximally confident correct ratings than those who did not hear a talk.

Table 28 - Results of GLM investigating relationship between participant confidence that captive conditions allow chimpanzees to express natural behaviours and potential explanatory variables (Independent variables). Significant variables shown in bold.

Independent Variable	F value (df)	p Value
Full model	(5, 159) = 1.68	.142
Experimental Group	**(1, 159) = 7.97**	**.005**
Frequency of Zoo Visits	(1, 159) = 0.05	.816
Education*Group	(2, 159) = 0.58	.559
Group*Visits	(1, 159) = 0.20	.658

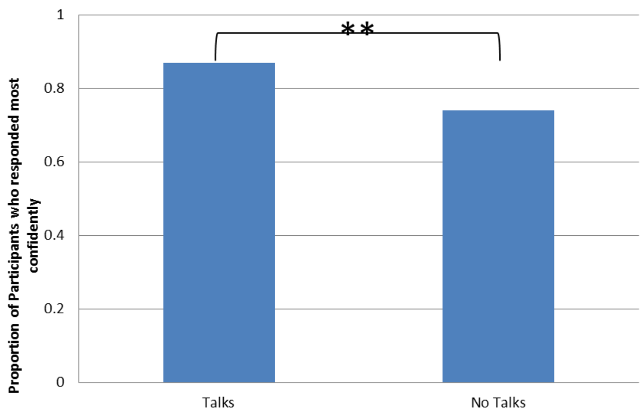

Figure 28 - Proportion of Participants who either attended or did not attend a chimpanzee talk that were maximally confident in the correct answer that captive conditions allow chimpanzees to express natural behaviours. ** P<.010.

Factors predicting adults' confidence level of responses to 'How important is it that captive conditions engage chimpanzees in activities that allow them to think?'

None of the factors explained a significant amount of variation in participant confidence of how important it is for captive conditions to engage chimpanzees in activities that allow them to think (Table 29).

Table 29 – Results of GLM investigating the relationship between participant confidence that it is important that captive conditions engage chimpanzees in activities that allow them to think and potential explanatory variables (Independent variables).

Independent Variable	F value (df)	p Value
Full model	(8, 3) = 2.28	.269
Experimental Group	(2, 3) = 0.42	.690
Frequency of Zoo Visits	(1, 3) = 0.01	.937
Education*Group	(3, 3) = 3.73	.154
Group*Visits	(2, 3) = 2.86	.202

Discussion

The results of this study suggest that 'Keeper Talks' are not particularly effective at transmitting educational messages about environmental enrichment within zoos. Attendance at a keeper talk where information pertaining to the correct answer was given did not significantly predict visitor responses to the majority of questions tested. Indeed it was quite surprising how many people got the incorrect answers to some questions, despite the correct answer being covered in the talk, just minutes before they completed the questionnaire. For example, only 9.4% of adult and 25.0% of young participants who attended the extended talk, where this information was provided gave a correct response to question pertaining to enrichment not having to look natural. Also discussed during the extended talk was information on the importance of enclosures being natural but we were unable to run statistical analysis due to only 4.7% of the adult and 0.0% of young participants who attended the extended talk selecting the correct answer that enclosures do not have to look natural. These results support the idea that zoo visitors generally believe naturalistic enclosures to be better for animal welfare (Seidensticker and Doherty, 1996) and the content of the extended talk did not cause the visitors to change their mind.

It is possible that 'Keeper talks' only work for disseminating 'new' information to the public and if they hold an existing opinion on a topic, it is unlikely that what is said during a talk will change their mind on this topic. The very small percentage (4.9% for adults and

0.0% for young people) of individuals who did not attend any talk and got questions related to natural looking enclosures correct indicates that zoo visitors have strong existing opinions that enclosures should look naturalistic. It is believed that attitude change may be unlikely in the face of new contradictory evidence, due to the fact that people do not judge evidence impartially (Lord, Ross and Lepper, 1979). When presented with information that both supports and contradicts existing attitudes, people seem to remember the strengths of the information that sits with their current views and the weaknesses of the information that does not (Lord, Ross and Lepper, 1979). This distortion of information often means that attitude change is unlikely (Cartwright, 1949). It is possible that if the questionnaire had asked participants what they had remembered from the talks rather than what they thought themselves we may have received different answers. The lack of effectiveness of the talks on topics on naturalistic enrichment and enclosures may either have been due participants not being convinced of the arguments within the talks or they may not have remembered the specific information.

Another possible explanation for why ‘Keeper Talks’ did not positively influence visitor knowledge on some questions could be the very high percentages of participants across groups who got the answer correct. This suggests an existing high level of knowledge about chimpanzees and animal welfare, meaning the talk was not providing new information for most visitors. For example, amongst the visitors who did not attend talks, 90.2% of adults and 100.0% young people knew that it was important that captive conditions engaged chimpanzees in activities that allowed them to think and that 100.0% of young people knew that it was important to ensure that the animals were allowed to express natural behaviours. The higher than expected levels of zoo visitor knowledge in some areas suggests that much of the information contained within ‘Keeper Talks’ may already be known by the visiting public and that these talks are not actually educating the public, in terms of providing them with new knowledge.

If ‘Keeper Talks’ are not necessarily providing visitors with new information, it is possible that they are consolidating existing knowledge and increasing visitors’ confidence that they know certain information. It was found that participants who attended ‘Keeper talks’ were more likely to give a maximally confident correct answer for the question asking if captive conditions allow chimpanzees to express natural behaviours than individuals who did not attend talks. However, hearing a talk had no effect on the confidence of adult visitors about the importance of animals having conditions that allow them to think. These results are equivocal and suggest that future research should be conducted that investigates in more detail if ‘Keeper Talks’ are increasing public confidence in their knowledge, perhaps through the use of entry and exit surveys.

My results also suggest that ‘Keeper Talks’ are not having any effects on the responses given to the questionnaire by young people. If ‘Keeper Talks’ are aiming to educate young people, this study suggests that this is not occurring. Future studies should focus specifically on how to tailor ‘Keeper Talks’ on environmental enrichment specifically towards young people, perhaps by distributing enrichment items to the animals during the ‘Keeper Talk’ or by encouraging visitors to make items, which could be given to animals as enrichment, at home and donating them to the zoo. The inclusion of examples of enrichment that young people can comprehend and even create themselves could improve the educational impact of ‘Keeper Talks’ for this key demographic.

Despite the negative results focussed on to date, I have also demonstrated that information about specific forms of enrichment can be effectively transmitted within ‘Keeper Talks’. The results from the question on the use of touchscreens as enrichment showed that people who heard the extended talk were significantly more likely than visitors in the standard talk or no talk groups to agree that touchscreens could be a good form of enrichment. During the extended talk the use of touchscreens as enrichment was compared with humans using a tablet computer, which is likely to have made this form of enrichment seem more concrete and less abstract. Even with the inclusion of this very specific example of non-naturalistic enrichment, visitors who heard the extended talk were not able to generalise this point and understand that enrichment does not have to look natural.

Music is another specific example of non-naturalistic enrichment that was mentioned during the extended talk, however, unlike touchscreens, none of the variables measured explained any significant differences in the opinions of the young people or adult visitors. The responses of the ‘no talk’ group indicate that zoo visitors did not tend to have particularly strong existing opinions about this form of enrichment being positive, so the failure of visitors to adopt the information given is likely not attributable to failing to change strong pre-existing opinions. I predicted that individuals who believed humans and chimpanzees were similar would also rate music as a good form of enrichment but this was not found to be the case. It seems more likely that people who were more informed about both topics gave correct answers to each of the questions. It thus remains unclear why visitors failed to remember or accept the information regarding music not being a successful method of enrichment for zoo housed chimpanzees that was offered in the extended talk.

As well as investigating the effect of different hearing different versions of a ‘Keeper Talk’ or no talk, I also looked at interactions between the experimental group visitors were in with their highest completed level of education and with how frequently they visit zoos. No interactions were found meaning that talks were not more effective for individuals who obtained certain educational levels or visited zoos frequently. This is a positive result for zoo education as it suggests that zoos do not generally have be concerned that they need to provide different information for individuals who may never have visited a zoo compared to more regular zoo visitors or those with different educational backgrounds. I did, however, find main effects of zoo visit frequency and age on one question. Significantly more visitors who visit zoos frequently (2+ visits/year) correctly answered that touchscreens were good enrichment for chimpanzees, than people who only visited a zoo once a year. This could be due to the fact that visiting zoos frequently increases exposure of individuals to the educational messages. Several studies (Adelman et al., 2000; Manubay et al., 2002; Dierking et al., 2004) found that a single zoo visit was not enough to change conservation related behaviours in visitors, suggesting that multiple zoo visits each year are required for educational messages to be fully assimilated. It was also found that within the young persons’ data, that older individuals were more likely to answer correctly that touchscreens were a good form of enrichment. Other than the two examples above, age and frequency of zoo visits did not affect the outcome of visitor knowledge.

Overall, this study suggests that ‘Keeper Talks’ are not particularly successful at providing young people or adults with new knowledge, with the content of talks only predicting zero out of three for young people and two out of five for adult visitor responses to questions examined. More research is needed to understand why the talks were successful in increasing knowledge on some topics and not others. I found some evidence that they may consolidate existing knowledge, leading to an increase in confidence in this knowledge, but further research needs to be conducted in this area. I have also found that existing visitor knowledge was very high on several topics, which was unexpected.

Due to the unexpectedly high visitor knowledge I decided to conduct a second study to investigate if zoo educators/presenters are aware of the knowledge levels of their visitors. Additionally, as I found that ‘Keeper Talks’ are not particularly effective at transmitting new information I wanted to understand if individuals in charge of 'Keeper Talk' content were intending for these talks to consolidate existing knowledge.

Study 2: Zoo Professionals

Aims and Research Questions

In this second study, I aimed to understand more about the perception of zoo visitor knowledge by individuals that work in zoos, including staff that deliver 'Keeper Talks'. I also aimed to comprehend the role of 'Keeper Talks' in zoos and if/how this affects the development of content for the talks.

In this study we aimed to address the following questions:

i) Are zoo professionals aware of the knowledge level of zoo visitors or do they misjudge it and are staff better at estimating the knowledge of the visitors to their own institution? This was investigated using a questionnaire, with zoo staff, asking them to estimate the percentage of zoo visitors that were able to correctly answer 10 different questions
ii) What do zoo educators/presenters believe the purpose of zoo talks to be and how do they decide upon the content of these talks? To answer these questions we conducted semi-structured interviews with individuals who were responsible for the provision of 'Keeper Talks' within zoos.

Methods

Ethics Statement

Participation in the study was completely voluntary and questionnaire responses were anonymised. Consent sheets were provided to obtain written consent and participants were given a debrief sheet after completing the questionnaire. The procedure was approved by the University of York regulated Department of Psychology Ethics Committee and the BIAZA research committee.

Questionnaire Participants

Individuals who attended the BIAZA Research Symposium on 27th and 28th June 2016, held at Yorkshire Wildlife Park, Doncaster, UK, who worked at an institution that had captive chimpanzees were invited to participate. After the questionnaires were initially distributed at the BIAZA Research Symposium, more responses were required, so questionnaires were sent directly to other British institutions housing chimpanzees to dispense amongst staff. In total, 30 responses were collected from five different institutions. Of the 30 individuals who completed the questionnaire, nine (eight keepers and one education officer) were known to actively give 'Keeper Talks' and 18 (11 keepers, one education officer, four head keepers, one Veterinarian, one Research and Conservation co-ordinator and one zoo administrator and research co-ordinator) were believed not to provide 'Keeper Talks' but regularly engaged with the public.

Interview Participants

Specific individuals working as heads of education or presentation departments at three British Zoos were approached and invited to participate in an interview relating to how the content of 'Keeper Talks' is decided upon.

Questionnaire Methodology

Zoo professionals were invited to complete a 10 item questionnaire (see appendix 9). The questionnaire contained the same questions that were included in the questionnaire given to zoo visitors in study 1. Zoo professionals were asked to imagine that 100 people who had visited their chimpanzee enclosure, but not attended a 'Keeper Talk,' at their institution had been asked questions that relate to effective enrichment for chimpanzees. They were asked to estimate the % of such visitors who would give the correct answer and were able to choose between percentage categories that ranged from 0 to 10% up to 90 to 100% .Three numbers on the Likert scale of 1 to 7 were underlined to indicate what we considered to be the correct answers for each question. The zoo professionals were also asked to give their job title and name of their institution so it was possible to measure the range of institutions covered by responses.

Interview Methodology

I conducted three semi-structured telephone interviews during August and September 2016 based around seven questions (see appendix 10) but further questions were asked depending upon the answers given by the interviewee. All interviews were recorded using an Olympus DM650 dictaphone and transcribed later using Olympus Sonority software.

Data analysis

Questionnaire

For each of the 10 items on the questionnaire the actual percentage of zoo visitors (both adults and young people) who had not heard a 'Keeper Talk' from study 1 that gave correct answers were compared with the percentages that the zoo professionals estimated to have given correct answers using one sample Wilcoxon signed rank tests. For analyses we used the middle values from the percentage category (e.g.35 would be used for 30 to 40) selected by the zoo professional and converted the visitor responses in the same manner (e.g. if 98% of visitors gave the correct answer then the value used was 95

Interviews

The responses given during the interviews were analysed qualitatively. Six themes were extracted from the responses of the interviewees.

Results

Questionnaire

The responses of the zoo professionals were significantly different from our sample of visitors to Edinburgh Zoo on eight out of 10 questions (Table 30). The two questions where the responses of the zoo professionals were not significantly different from the sample of visitors were 'Are touchscreens good enrichment?' and 'Is music a good form of enrichment?'. When looking at the eight questions where the responses of the zoo professionals were significantly different from the sample of visitors, the knowledge of zoo visitors was under-estimated by the majority of zoo professionals for five questions and their knowledge was over-estimated by the majority of zoo professionals for three questions (Table 30; Figure 29). I also examined the responses of staff that worked at Edinburgh Zoo compared to staff at other institutions to see if zoo professionals are more accurate at estimating the knowledge of the visitors at their own institution than those from another. Edinburgh Zoo staff gave estimates that were closer to the actual percentage of visitors that answered the questions correctly for four out of the eight questions where the responses of all zoo professionals were significantly different from the visitor sample (table 31).

Table 30 – Results of One-sample Wilcoxon Signed Ranks tests comparing the estimates of Zoo Professionals (ZP) on the knowledge of Zoo visitors with actual zoo visitor knowledge.

Question ZP Estimated the Percentage of Visitors knew the Answer to	One-sample Wilcoxon Signed Ranks Test (p value)	% of ZP Correctly Estimated the Level of Visitor Knowledge	% of ZP Under-estimated Visitor Knowledge	% of ZP Over-estimated Visitor Knowledge
Do humans and chimps share more or less than 90% of our DNA?	<.001	10	90	0
How similar do you think the mind and behaviour of humans and chimpanzees are?	.006	10	23.3	66.7
Is knocking on windows a good form of Enrichment?	<.001	16.7	83.3	0
Are touchscreens good Enrichment?	.246	13.8	41.4	44.8
How important is it to make the enclosure look as similar to the animal's natural habitat as possible?	<.001	13.3	0	87.6
How important is it to ensure that the animals are allowed to express natural behaviours?	<.001	13.3	87.6	0
How important is it to ensure that the animals are always visible to visitors?	<.001	6.9	82.8	10.3
How important is it for Enrichment is similar to something the animals would experience in the wild?	<.001	3.3	0	96.7
How important is it to engage the animals in activities that require them to think?	<.001	10	90	0
Is music a good form of Enrichment?	.364	26.7	36.7	36.7

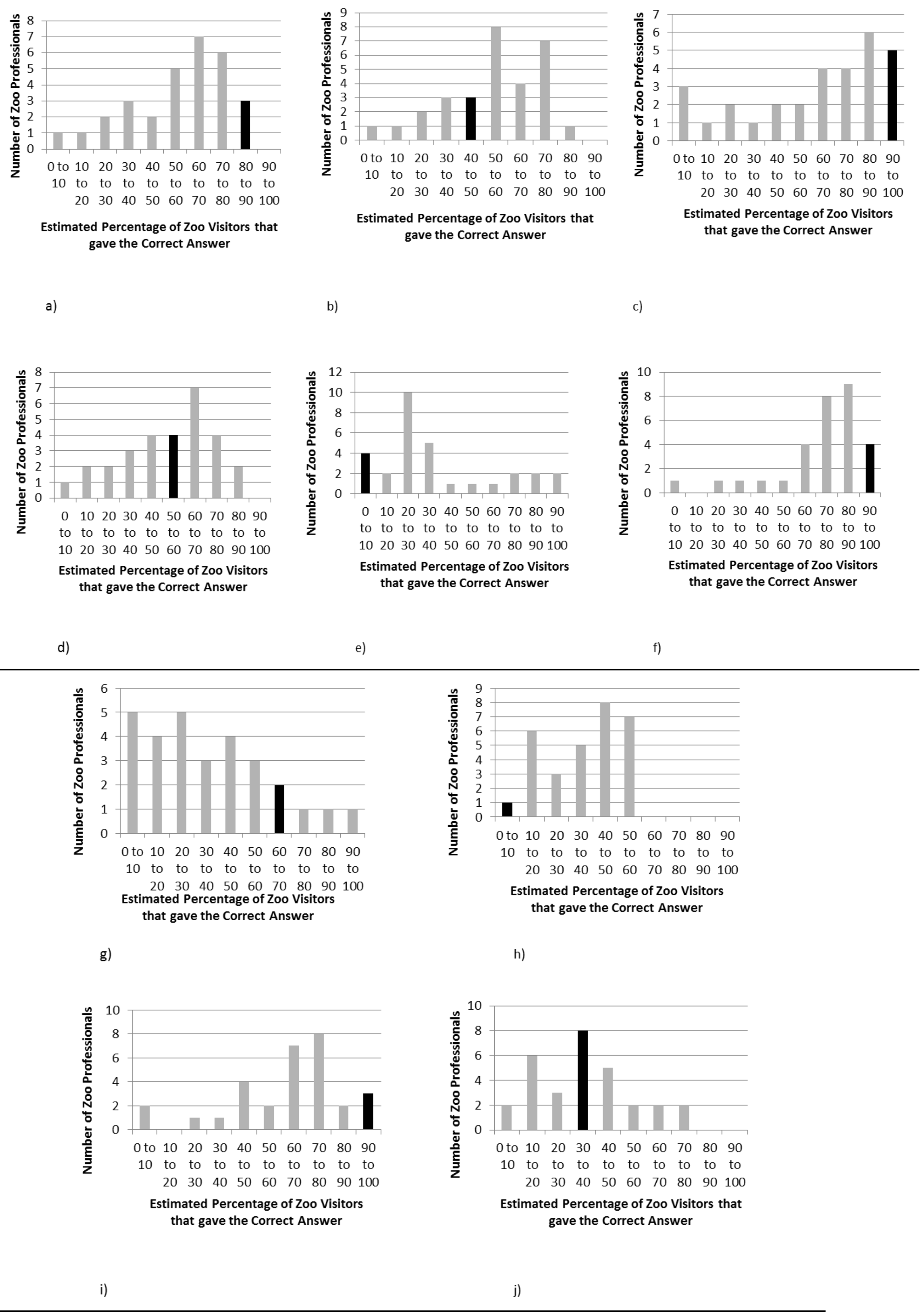

Figure 29 –Bar graphs showing the distribution of the number of Zoo professionals that selected each percentage category for visitor knowledge for each of the ten questions (a to j). The category with the correct percentage of visitors who gave the correct answer is indicated with a solid black bar.

Table 31 – Median estimates by staff at Edinburgh Zoo and four other institutions of the percentage of visitors to Edinburgh Zoo that answered the questionnaire questions from Study 1 correctly. This includes data for the eight questions where the responses of zoo professionals were significantly different to those of the zoo visitors.

Question Zoo Professionals Estimated the Percentage of Visitors knew the Answer to	Median of Edinburgh Zoo Staff Estimates	Median of Estimates by other Zoo Professionals	Actual Percentage of Edinburgh Zoo Visitors that Answered Original Questionnaire Correctly
Do humans and chimps share more or less than 90% of our DNA?	65	55	85
How similar do you think the mind and behaviour of humans and chimpanzees are?	55	55	45
Is knocking on windows a good form of Enrichment?	75	65	95
How important is it to make the enclosure look as similar to the animal's natural habitat as possible?	35	35	5
How important is it to ensure that the animals are allowed to express natural behaviours?	85	75	95
How important is it to ensure that the animals are always visible to visitors?	25	45	65
How important is it for Enrichment is similar to something the animals would experience in the wild?	45	45	5
How important is it to engage the animals in activities that require them to think?	75	65	95

Interviews

Target Audience(s)

All of the interviewees stated that the 'Keeper Talks' at their institutions were aimed at a wide range of ages and backgrounds, even people with no prior knowledge of wildlife. One stated that the talks were aimed so that children of seven and older could understand what was being said. Additionally, they aimed for their talks to be understood by people who were able to follow spoken English but are not necessarily native speakers.

Main aim(s)

Interviewees all indicated that 'Keeper Talks' have multiple aims that they felt were equally important. These multiple aims were; consolidating existing public knowledge, presenting new information, providing something enjoyable for visitors, spreading conservation messages and creating interest/enthusiasm/empathy for animals. The idea of creating an opportunity for visitors to 'slow down' was mentioned by one individual. The idea behind this was to give the visitors time to actually observe animal behaviour, really think about what they were seeing and possibly allow them to have a 'wow' moment with the animals. The 'wow factor' was also mentioned by another interviewee in relation to what they hoped the facts presented in their talks would have.

Talk content

In each of the interviews it was mentioned that there was is a basic set of information that presenters were provided with, which covered the facts and conservation issues that the Education/Presentation department wanted to be covered. This also ensured that what was delivered was not too full of facts to stop it from being engaging. The lack of an exact script did, however, lead to some variation in what was covered between individual presenters. One participant brought up the point that a good presenter would tailor what information was covered depending on the audience present at the time or what the animals were doing. The audience would also find it more engaging and natural if a set script weren't being followed.. Following a set formula for all talks meant that visitors could tell when the 'boring conservation bit' was coming and could walk away before the end. They also stated that, unfortunately, not all individuals who gave 'keeper talks' had the skills to be able to tailor talks to a particular audience whilst making it appear natural. This could lead to them seeming boring and the visitors not assimilating the information. The amount of help for improving these skills seems to depend on the job role of the individual giving the talk. Those who worked in Education/Presentation departments may have had the opportunity for one-on-one feedback with managers and were often willing to make improvements. It generally appeared that zoo keepers who gave talks as a very minor part of their job were less likely to be given such opportunities and were not always as concerned about trying to improve even if the opportunities were available.

The frequency of changes to talk content

The responses to this varied but generally seemed to occur between every six months to a year and the alterations were mostly in response to changes to the animal collections, such as births or deaths. Departments appeared to allow presenters the freedom to add any new information they found about the species from the media or scientific journals. It was pointed out that if the department wished for content to be changed this could be difficult. The individuals giving the talks may not have had the time to amend the content or may have viewed giving talks as only a minor part of their jobs and not be willing to put in the extra work to make and learn these changes. Additionally, some staff may not appreciate comments about changing content of their talks and may feel as if they are being criticised.

What informs the changes to content?

The reoccurring answers given by the interviewees were that the publication of new scientific information about a species and commonly asked questions by visitors lead to departmental changes in the content of talks. In an attempt to make talks more engaging one respondent mentioned that recently their institution changed the content and presentation of their talks to give them a political theme during the run up to the British General Election, making them seem relevant to current affairs. Whilst visitor comments were highlighted as being a positive way of receiving feedback on talks and their content, especially when they praised what is being done or showed that visitors have learnt something, they are unlikely to inform changes to the content of 'Keeper Talks'. This is because visitor comments related to content often request more 'performing' animals, which is a direction many zoos are keen to move away from.

Assessment of impact of talks or current knowledge of visitors

All interviewees mentioned that some assessment had been done on both the success of their talks and the knowledge of their visitors. However, it appeared that any assessment did not happen frequently as it was difficult to conduct due to staff shortages or a lack of funding.

The majority of methods of assessment that were mentioned during the interviews were related to identifying if 'Keeper Talks' were able to provide something enjoyable for visitors. Questionnaires were used to ask visitors about aspects of talks they liked or didn't like and comments from visitors, especially via social media or TripAdvisor, were mentioned as a positive method of obtaining feedback. The departments responsible for talks, or individuals delivering them, could benefit from positive comments received in this way as they were very visible to zoo management and recognition for good work could be attributed. However, one interviewee felt that this form of assessment could have too much importance placed upon it by management whilst potentially under-valuing information obtained via other assessment methods.

One interviewee mentioned that staff had previously attempted to overhear what visitors were talking about amongst them after the talk had ended, to hear if they were making positive comments about the animals. Comments such as "They are so cute" or "Aren't they interesting?" could imply the combination of the talk and observing the animals for a few minutes had created interest/enthusiasm/empathy for the animals. Staff members had also used this technique to establish if visitors had learnt new information that they then discussed within their group. It was stated that this has been used to improve the existing practice of presenters and to report to zoo management on visitor learning, empathy and enjoyment. However, it was not clear if this form of reporting to management was a formal or informal process.

During the interviews it was mentioned that another method of assessing if 'Keeper Talks' presented visitors with new information was the use of questionnaires that compared existing visitor knowledge at the start of a zoo visit with what they had learnt by the end. Visitors had been asked to recall any specific information they may have learnt from a 'Keeper Talk' or during their visit generally. One interviewee recalled using questionnaires on one occasion to assess both existing knowledge and if visitors had learnt new information , however, due to the questionnaires being conducted both physically and temporally close to the 'Keeper Talks' the responses appeared very positively skewed towards the impact of the talks. These positive responses could possibly have been due to a form of response bias, which is where questionnaire or interview participants want to provide the interviewer with the answers they think the interviewer wants. Information about how these responses were used by the institution was not provided but it was stated that this form of assessment was not replicated.

None of the assessment methods mentioned were directly related to assessing whether conservation messages were being spread, although listening to visitor conversations and questionnaires could be used to address this aim. However, one interviewee stated that their staff members that delivered 'Keeper Talks' recorded estimates of the number of people that attended each talk as well as what percentage stayed until the end. This response was provided by the individual who stated that almost all of their talks contained a conservation message, which suggested that the percentage of visitors who stayed until the end of the talks would have been present when the conservation message was mentioned. However, as it is impossible to know if any or all of those individuals had paid attention, remembered the information or felt compelled to change their behaviour, this measure does not truly assess the impact of the talks. It could be argued that recording the estimated percentage of visitors who have stayed until the end of the talk indicated the level of visitor enjoyment of the talks, as visitors who choose not to stay to the end may well have chosen to leave due to a lack of enjoyment.

General comments

During the interviews some comments were made that did not fit into specific themes but are still worth mentioning. It was touched upon that the using the word 'talk' can sometimes lead to visitors being discouraged from attending as they feel that it may be too much like a lecture. In this instance having an active element and calling it a 'feed' may have avoided such problems. However, active elements can sometimes lead visitors to view animals as performers rather than wild animals. Additionally, comments that were made highlighted the need for talks to be given by well-trained and engaging individuals as they felt that this would ensure the maximum likelihood of information being transmitted to visitors. Although intuitive, systematic empirical data is lacking to support the influence the skill of the presenter has on information retention or attitude change.

Discussion

The results of the questionnaire study suggest that zoo professionals, including those who deliver 'Keeper Talks', do not have a very accurate understanding of what zoo visitors already know. Out of a total of ten questions, there were only two questions (on touchscreens and music as forms of enrichment) where the zoo professionals' answers were not significantly different from the percentage of visitors who gave the correct answer. The data displayed in figure 29 indicates that for three of the eight questions where the zoo professionals gave significantly different responses from the zoo visitors, the zoo professionals were over-estimating visitor knowledge but they under-estimated it for five of the eight questions. I also found for half of those eight questions, staff at Edinburgh Zoo descriptively gave more accurate responses than staff at other institutions. This indicates that some of the inaccuracy of staff from other institutions may be due to variation in visitor knowledge across institutions, but when taken together, these results suggest that zoo professionals are not particularly accurate at estimating the levels of knowledge of zoo visitors generally or at their own institution. If ‘Keeper Talks’ are aiming to present new information to visitors, it is very likely that what talk content creators believe to be new information may be something that visitors already know.

All three interviewees stated that ‘Keeper Talks’ were aimed at all zoo visitors, including children and young people. The results from study one suggest that these talks may not be effective at delivering messages to these younger groups of visitors, as attending a ‘Keeper Talk’, compared to not doing so, did not have any effect on the likelihood of individuals aged 6 to 21 giving a correct answer. This suggests that further research at multiple institutions should be conducted on the educational impact of such talks purely for this age group to establish how this educational tool can be used more effectively for such a key demographic.

Presenting new information was referred to as one of the main aims of ‘Keeper Talks’ as were consolidating existing public knowledge, providing something enjoyable for visitors, spreading conservation messages and creating interest/enthusiasm/empathy for animals. Having multiple aims for these talks can be problematic compared to having one clear, specific aim, especially as ‘Keeper Talks’ are generally around 10 to 15 minutes in length. This means that there is little time to address each of the aims and increases the chance that none of them will be achieved. It is, therefore, very important, to evaluate the ability of the talks to achieve each of these aims. Unfortunately this does not seem to occur frequently, most likely due to a lack of time or resources. Whilst several different methods of assessment were mentioned as being used at the three institutions, it seems likely that comments from visitors via TripAdvisor or social media will become the most commonly used tool for feedback from visitors, due to such importance being placed upon it by senior management and the popularity of such sites by the public for planning days out. However, it does not seem that this is a successful method for measuring the educational impact of ‘Keeper Talks’. When looking at TripAdvisor reviews for zoos, reviewers more frequently comment upon price of entry tickets, food outlets and overall enjoyment of the day than ‘Keeper Talks’ and if they are mentioned the reviews will most commonly refer to visitor enjoyment of them rather than stating if anything was learnt. Future research could be conducted to see if social media and TripAdvisor could become a useful tool for education assessment by having ‘Keeper Talks’ presenters asking visitors to use social media to comment on one thing that each visitor has learnt during their day at the zoo as part of the talks.

With regards to the content of ‘Keeper Talks’, there seems to be much effort put into ensuring that the information presented is fairly consistent and not too information dense whilst avoiding having presenters sticking to a rigid script that may negatively affect visitor engagement. As the talks are aimed at everyone from the age of seven upwards, the content cannot be overly scientific or contain words that a primary school child is unlikely to be familiar with. However, the interviewees did mention that new scientific knowledge about talk species may lead to changes in content, depending on individual presenters, but this information is likely to be presented in a very accessible manner. One institution stated that they try to include facts that deliver the ‘wow factor’; possibly being information that the public may not have heard before. However, as with evaluating impact, assessment of this content appears to happen very infrequently. With the results of the questionnaire study showing that zoo professionals are under-estimating visitor knowledge, this suggests that more studies should be undertaken by each institution to be able to tailor their talk content to their audiences.

The interviewees also highlighted the importance of the skills of a good presenter, whilst acknowledging that not all individuals that deliver ‘Keeper Talks’ have these skills. It is currently not known if having good presentation skills affects the retention of knowledge in addition to levels of engagement but if future research establishes a link between the skill level of presenters and knowledge retention institutions should place more importance upon training staff to develop such abilities.

Overall, the results of the questionnaires and interviews highlight the need for much more research into establishing existing visitor knowledge at each institution to ensure that ‘Keeper Talks’ are appropriate for their audience, including young people. Additionally more resources need to be invested into systematic assessment of whether the talks are meeting their educational aims, with action taken to change the talks or modify the aims if data highlights deficiencies. It may be that keeper talks increase engagement with the animals and visitor enjoyment, but are not successful at changing knowledge, attitudes or behaviour. If this is the case their place as an educational tool, helping fulfil the educational remit of a zoo, may need to be re-evaluated.

Conclusions

This is the first study to investigate the effect of ‘keeper talks’ on educating the public about welfare and enrichment for zoo-housed chimpanzees. I have shown that it is possible for these talks to change public opinions on some forms of enrichment that do not contradict existing knowledge. However, they did not appear be effective for transmitting information relating to natural-looking enrichment and enclosures. This may have been because visitors were not persuaded to change their existing opinions or they may not have remembered the specific information that was presented during the talks. I also found that zoo professionals appear to be inaccurately estimating the existing knowledge of visitors highlighting the need for more research into visitor knowledge to ensure talks are pitched appropriately. It is suggested that more time and resources need to be allocated for undertaking evaluations into visitor knowledge and the various potential impacts of ‘Keeper Talk’ using a variety of rigorous empirical assessment measures. Reliance on feedback via social media is likely to focus evaluation of keeper talks against the goals of visitor enjoyment, whilst neglecting their potentially important educational role.

Chapter 7: Discussion

Summary of Results

The research undertaken during my PhD aimed to evaluate the impact of the modern zoo on two species of great ape: chimpanzees and humans. For zoos to endure they need to be a place for both species to thrive. Currently many zoo-housed chimpanzees display many abnormal behaviours and those indicative of anxiety (Birkett and Newton-Fisher, 2011). In chapter 3 I have investigated possible causes of three of those behaviours; yawning, scratching and R/R. In doing so I have found several possible triggers for two them. R/R appears less likely to be a behaviour that is triggered by current social events or animal management practices; instead it seems to be a behaviour that has persisted from previous distress. R/R also appeared to decrease in prevalence in the BB chimpanzees after their move to Edinburgh, possibly due to moving to an enclosure that allows a complex social group to engage in fission-fusion behaviour. This suggests that providing a physical and social environment that allows species-specific behaviours to be displayed can improve welfare and reduce the performance of behaviours that can lead to poor-health.

As well as focusing my research into potential reasons for the occurrence of specific unwanted behaviours, I have also investigated whether a commonly used form of 'enrichment' does truly lead to positive welfare changes for chimpanzees. The results discussed in chapters 4 and 5, unlike those of Howell et al. (2003) and Videan et al. (2007), suggest that music is not having an enriching effect upon zoo-housed chimpanzees and that individuals in both a zoo and a laboratory do not display any form of preference for music or silence. It is hoped that these results will be disseminated and will result in changes to enrichment practices in zoos that may not currently be having the desired or indeed expected effect upon chimpanzees' welfare.

The need to improve the welfare of zoo-housed animals is in part due to the presence of visitors in zoos and these visitors are necessary to provide public funding for conservation projects supported by zoos.. The public support of conservation projects, both monetarily and through behaviour changes, is also dependant on the provision of zoo-based education to create understanding of animal species, the threats they face and empathy towards these animals and their welfare. The results of chapter 6 suggest that 'Keeper Talks' may not currently be an especially effective method of educating members of the visiting public. If zoo education generally is not achieving this then it could be argued that the cost of exposing animals to large numbers of humans on a regular basis is not offset by the benefit of educating the public.

In the discussion sections of each of my chapters I have talked about the findings as well as the limitations of each of the studies. Here I shall attempt to draw wider conclusions about this research and recommendations that can be presented to zoos to improve and enhance conditions for both of my study species.

How do we prevent R/R in zoo-housed Chimpanzees?

Regurgitation and reingestion (R/R) is abnormal behaviour observed in zoo-housed chimpanzees that can cause serious health problems (Wyngaarden et al., 1992) yet so far no individual trigger has been identified as being responsible for the performance of this behaviour. The research in chapter 3 suggests that there is no specific trigger for this behaviour in the Beekes-Bergen individuals at Edinburgh Zoo. Instead I believe that it is likely to have developed during previous captive experiences as a result of suffering distress. The animal then adopts R/R as part of its learned behavioural repertoire, and will continue to engage in R/R, albeit at a reduced level, even once the welfare of the animal has improved. This means that the only way to eradicate this behaviour in chimpanzees, as well as other zoo-housed primates, is to ensure animals are protected from distress and poor welfare for their entire lives.

A very positive finding from this research is that R/R does not appear to be socially learnt in the same way that coprophagy is believed to be transmitted (Hopper et al., 2016). This is encouraging as it means that relocating individuals that engage in R/R for breeding purposes hopefully will not lead to the behaviour spreading into a new group, as was shown with the immigration of the BB individuals to Edinburgh Zoo. Additionally, it appears that R/R is not transmitted vertically. Velu was born on 24th June 2014 to Heleen, a BB individual who has been known to engage in R/R since 2009. With a mother, suspected father (Rene) and four other individuals in the group who regularly engage in R/R it may have been expected that the infant would have an innate disposition towards engaging in the behaviour, or learn the behaviour from observing his mother and the other individuals. Velu is currently over two years old and has never been recorded as engaging in R/R by any of the researchers collecting long-term behavioural data at Budongo Trail. The continuation of this long-term data will facilitate developmental studies investigating how often Velu has observed this behaviour and, if he does ever begin to engage in R/R, this data may be able to elucidate the developmental trajectory of the behaviour in chimpanzees.

One possible reason for Velu not yet being observed engaging in R/R, as well as the decrease in R/R rates detected in the BB individuals from 2009 to 2015, is the design of the Budongo Trail enclosure. When it was completed in 2008 it had been created to facilitate vocal and rhythmic communication, allow individuals to avoid the public gaze and enable the formation of a large, socially complex group of chimpanzees. Enclosure design is a vital part of the welfare of a captive animal. Zoos with existing enclosures should be disseminating information about both the positive and negative aspects of their designs, to benefit the creation of improved enclosures. If it is not possible for an institution to rebuild an enclosure for their animals but they wish to make changes to improve the welfare of its inhabitants there is now a digital tool that can make pertinent suggestions. The Enclosure Design Tool (EDT; Thorpe, 2016) is able to make suggestions about a specific enclosure to allow the chimpanzees within the enclosure to develop behaviours more akin to that of wild chimpanzees. The EDT developers aim to increase the scope of the tool within the next five years to cover other great ape species. This tool can generate quick positive welfare changes (Thorpe et al., 2016) and the proposed adaptations of enclosures are likely to cost much less to implement than re-designing and re-building an enclosure from scratch, ultimately benefitting both the animals' welfare and reducing the fiscal impact on the zoo.

Improving the designs of chimpanzee enclosures is crucial for the progression of zoo welfare but it is equally important that zoos worldwide are aware of the existing negative or abnormal behaviours their animals are displaying before they can make any changes to potentially benefit those animals. This problem was recently discussed at the IPS/ASP Conference (Bloomsmith et al., 2016), where a relatively simple, standardised survey was highlighted as a possible method of gathering data on such behaviours in chimpanzees. The tool has so far been used with 726 individual chimpanzees in zoos, laboratories and sanctuaries. 56% of the animals displayed at least one abnormal behaviour; 24% of those performed coprophagy and 11% were observed to engage in R/R (Bloomsmith et al., 2016). As of 2013, there were approximately 1560 chimpanzees in zoos and research facilities across the world (ISIS.org, 2013; Conlee, 2007) and yet more in sanctuaries. Extrapolations of Bloomsmith's results suggest that there are at least 874 chimpanzees in captivity that display one or more abnormal behaviour. It is worth noting that 78% of chimpanzees in zoos displayed abnormal behaviours compared with 50% of those in laboratories and 46% in sanctuaries. This difference between zoos and laboratories could be due to the fact that laboratories must follow strict guidelines on caring for their animals, suggesting that zoos need greater regulation of care for their chimpanzees. Another possibility could be that the abnormal behaviours displayed by the individuals in zoos may be indicators of previous rather than current distress. Whilst the survey can quickly identify very obvious behaviours that chimpanzees may engage in, it could be much harder to identify more subtle behaviours or those that happen quickly, such as R/R, suggesting that the 11% who were observed engaging in R/R may be an under-representation of the actual number of animals who engage in the behaviour. The survey does not state the duration of observations required before it can be completed and, as such, it is likely to be completed based on what staff have happened to have observed whilst undertaking their duties rather than during periods of in depth observations. So far the tool has been used by facilities in the USA but a similar tool could be used for British and European zoos. Despite there being some minor drawbacks with the current version of the tool, having a more comprehensive understanding of the types of complex behavioural problems faced by captive chimpanzees would enable the provision of changes specific to individual needs. The use of enrichment tailored to explicit behavioural needs can be very effective but when a form of enrichment is used in the hope that it will generally improve animal welfare it becomes much less successful.

How do we improve the provision of Enrichment in zoos?

The four studies, conducted at two research sites, reported in chapters 4 and 5 demonstrate that music is not an effective form of enrichment for zoo-housed captive chimpanzees. These results support recent research conducted by Ritvo and MacDonald (2016) with zoo-housed orangutans. They conclude that not only is music not enriching but it cannot be distinguished from noise (scrambled versions of clips of music) by orangutans. My results, however, contrast those of Howell et al. (2003) and Videan et al. (2007) who argued that music had positive effects on their laboratory-housed chimpanzees, for example increasing social interaction and decreasing aggression. As neither of these studies allowed the chimpanzees the option to escape the music if they wanted to, unlike in my research, it is possible that the behavioural changes they found were part of a coping strategy to the music. However, as these studies were conducted in laboratories, it could be possible that the music broadcast was able to mask other distressing noises in the environment and negate the effects of aversive stimuli. It is also important to highlight that my research showed that playing classical and pop/rock music whilst providing an silent ‘escape area’ did not cause any negative welfare effects. I would not therefore suggest the immediate abandonment of music enrichment for primates but would recommend that its presence is scientifically analysed for enriching effects in more species and settings; something cannot be considered to be ‘enrichment’ unless it is truly enriching for an animal. Equally, if music is heard by a group of animals, the analysis should be conducted on an individual level to ensure that it is not having a negative effect on a minority, which can easily be masked when using group analysis (Wallace et al., 2013). I would advocate this approach to the use of all forms of enrichment, especially within zoos where peer-reviewed empirical studies of forms of enrichment are less common (de Azevedo, 2007).

One of the drawbacks with enrichment studies is that they are frequently conducted on animals that are already distressed or have complex behavioural issues. As such, if a form of enrichment is ineffective for the circumstances of specific individuals, that enrichment could be dismissed for an entire species. A way of counteracting this issue is the previously mentioned concept of selecting enrichment to provide a behavioural need for an animal, rather than doing something to occupy their time and potentially reduce boredom. An extension of this concept would be ‘preventative enrichment’, where enrichment is used to promote species-typical behaviour or to address a behavioural need that is commonly seen in captive animals of that species but this is done with individuals that have not yet developed abnormal behaviours. This could lead to a new generation of chimpanzees that would never be seen to engage in commonly observed abnormal behaviours like hair plucking. This would require a change in mentality towards enrichment, where it would no longer be viewed as method of improving welfare for animals but a system of preventing poor welfare.

This captive chimpanzee utopia is unlikely to come to pass in the near future but positive steps are being taken within the enrichment community. The ‘Shape of Enrichment’ is an organisation that promotes knowledge and techniques across the world, including to facilities in countries where animal welfare has not traditionally been of great importance. Additionally the organisation’s website contains a database of enrichment ideas, for numerous species, which have been viewed to be successful. This allows caregivers the option to search for forms of enrichment for the species of animal they work with. There is also a second database detailing enrichment devices or interventions that have not worked or has led to an animal becoming injured and/or dying. Unfortunately, whilst institutions are keen to share or publicise their successes, they are much less willing to share any ‘failures’, however, this is a vitally important resource that can help to prevent future enrichment related accidents. It is worth noting that the majority of entries in the databases are based on keepers’ impressions as to whether or not the form of enrichment is successful, rather than empirical data. As such, animals may have appeared not to interact with a device even though it had positive effects on behaviour (Reimer et al., 2016) leading to it being incorrectly categorised as unsuccessful or vice versa.

We should, therefore, address the current methods used for assessing enrichment and animal welfare generally. As mentioned in the introduction to this thesis, there is no single accepted method for measuring animal welfare and those that are currently used all have disadvantages. In chapters 3 and 4 I used behavioural measurements of welfare but they can be problematic to interpret. For instance, in chapter 3 I looked at possible triggers for yawns as they are believed to be an indicator of anxiety in primates (Maestripieri et al., 1992; Troisi 2002). However, non-human primates display two forms of yawns; full yawns and yawns where muscles are modified to prevent the mouth from opening fully (Vick and Paukner, 2010). The latter is associated with anxiety but the former is thought to be a form of threat display as the canine teeth are revealed and this behaviour is more frequently displayed by males than females, but only in species that exhibit canine sexual dimorphism (Schino and Aureli, 1989). Additionally, it has been demonstrated that yawning in chimpanzees can be contagious (Anderson et al., 2004). Whilst it is possible that ChimpFACS (Vick et al., 2007) could have been used to distinguish between full and half yawns, it was not possible to use this system as part of my research and it is, therefore, likely that some of the yawns that were recorded in the data were falsely attributed to the individual chimpanzee being anxious.

As behavioural measures of animal welfare can be problematic, a combined approach using physiological measures could create a stronger methodology. As discussed during the thesis introduction, measures such as faecal/urinary cortisol can fluctuate without the presence of a stressor and the restrictive price for analysis equipment means that it is unlikely to be adopted as a ubiquitous method for assessing zoo animal welfare. Recent technological advances have shown that measuring eye temperature using infrared thermography is a quick and effective method for assessing stress in animals that may not

be detected using behavioural observations (Yarnell et al., 2013). This method is non-invasive and gives an instant indication of the level of stress an animal is experiencing. This technology could be easily used within zoos to quickly establish if potential stressors, such as visitor presence, are actually leading to animals experiencing stress.
The use of infrared technology may be part of the future of stress and welfare assessments in zoos but I would argue that they cannot be the sole assessment method as it cannot be used for establishing whether an animal is experiencing good welfare. Good welfare is not the absence of suffering or stress but having a positive quality of life. Boissy et al. (2007) highlighted the importance of identifying the positive emotions displayed by captive animals to establish when that animal is experiencing good welfare.

A method for assessing aspects of both good and poor welfare is using specific welfare questionnaires. Previous studies using subjective measures of animal welfare have relied on the use of questionnaires that have been modified from existing human questionnaires for use with captive primates (Weiss et al., 2011) leading an anthropomorphised view of animal welfare. A recently created welfare questionnaire has been used with captive capuchins (Robinson et al., 2016) and chimpanzees (Robinson, in prep), which aims to avoid this issue. The questionnaire was specifically created for use with captive animals, based on the idea that social relationships, cognitive stimulation, stress, health and control over the environment are the largest contributors to an animal's quality of life (McMillan, 2005). As such, the questionnaire is able to capture information on both positive and negative aspects of an animal's welfare. The questionnaire has been validated using long-term behavioural data on zoo-housed chimpanzees; higher scores on the questionnaire (an indicator of poorer welfare) were associated with higher incidences of abnormal behaviours such as R/R and urine drinking. As this 12-item welfare questionnaire can be conducted by animal caregivers in a relatively short amount of time, this is another method of welfare assessment that could be used in zoos to quickly identify any animals that are suffering or experiencing lower welfare as well as those experiencing good welfare.

In the future, I hope that the use of enrichment in zoos will become more evidence-based and with relatively quick and simple ways of assessing welfare now available, this should make the prospect less daunting for animal caregivers. Ideally this will lead to more appropriate provision of enrichment that will contribute to higher levels of welfare for zoo-housed animals, as well as those found in other facilities.

How do we educate zoo visitors?

As with enrichment, the results of chapter 6 advocate that zoo education too becomes more evidence-based. Whilst the chimpanzee 'Keeper Talks' delivered at Edinburgh Zoo were effective at transmitting the message that touchscreens are an effective form of enrichment for chimpanzees to adult visitors, they did not appear to have a significant effect upon the knowledge of young people. I have also found that zoo professionals do not generally have an accurate estimate of the existing knowledge of the zoo-going public. In order for 'Keeper Talks' and other forms of zoo education to actually provide visitors with new information, those deciding upon educational content need to regularly assess existing visitor knowledge and the impact of their education methods. It was highlighted by interviewees that such assessment can be difficult due to a lack of time and/or funding. Due to the importance placed on zoo education by the World Association of Zoos and Aquaria (WAZA, 2005), more pressure could be applied to zoos to find the time and resources to make their education programmes more effective. Alternatively, more innovative and relatively cheap methods of educational research with visitors, such as the use of social media, could be introduced.

One issue that could hinder visitors self-reporting on what they have learnt from the zoo is that most people visiting a zoo, just want to have an enjoyable experience (Morgan and Hodgkinson, 1999). This may in part explain why no effect of attending a 'Keeper Talk' was found on visitor knowledge in study 1, as if the primary reason for attending the 'Keeper Talk' was related to enjoyment then the public may not have concentrated on the content of the talk and instead viewed it as an opportunity to observe the chimpanzees being fed. If this is the case then it leaves zoo educators with two options; trying to rebrand zoos as places of learning to make them appear similar to museums and art galleries or taking advantage of visitors wanting an enjoyable experience to provide educational opportunities. As zoos require visitor entry fees to continue running, as well as to support research and conservation projects, the second option makes more financial sense but what other methods of educating visitors can be provided within zoos that can capitalise on visitor enjoyment?

Interactive devices were highlighted in chapter 1 as an educational tool that visitors engage with more than static signage (Lukas and Ross, 2005). One recent study used such devices to display educational games, installed at Marwell Wildlife and Edinburgh Zoo, aimed to increase interest in psychology, research conducted within zoos and primatology (Whitehouse et al., 2014). The games were designed to appeal to young people under the age of 16 but adults of up to the age of 68 were recorded playing with them. The study found that 24% of visitors who entered the area with the interactive device actually played the games, which is much higher than the 9% that Ross and Gillliespie (2009) observed interacting with static signage. The games also increased interest in science and knowledge of primates, especially in the target age range of under 16s. This shows that interactive devices and games are a better educational resource that traditional signage. Also, with the increase of touchscreen technology within the home, work and learning environments, it is likely that zoos will become much more dependent on such interactive devices to communicate with their visitors.

Whilst interactive devices are an updated version of signs, which have been present in zoos since they began to open to the public in the late 1800s, there are also very novel ways that zoos can potentially educate their visitors. The vast majority of zoos in the UK have at least one childrens' play area but they are usually fairly generic and unrelated to the zoo environment in theme. I believe that so far there has been no research conducted on the use of themed play areas or equipment to educate children of different ages, especially within zoos. This potential form of education could be especially effective for younger children between the ages of two and five that are less likely to pay attention to other, traditional forms of zoo education. Research on play during early childhood has shown that when children experience a novel theme of play setting, for example a jungle or under the sea, this stimulates more sophisticated styles of dramatic play (Howe et al., 1993; Woodard, 1984). Additionally, it has been postulated that the environments children play in tells them about who they are and what they want to be (Cohen and Trostle, 1990). This research suggests that not only could a zoo appropriate themed play area benefit child play development but it could also affect their sense of their future selves, potentially leading to more empathy towards animals or more desire to conserve species. This is an area of research that could be undertaken across multiple zoos due to the ubiquitous nature of play areas within zoos, and the frequent need to replace areas that are damaged or no longer look appealing.

Research has recently been conducted on the effectiveness of educating young children, aged three to six, using a specially designed show (Spooner et al., 2016). The production made use of puppets, digital media and contemporary pop/rock songs, that children would be familiar with, where the original lyrics had been altered to include conservation related messages. Participants in the study had their knowledge tested before and after watching the performance and it was found that, on average, they were able to correctly answer 20% more of the questions. This research suggests that such displays can be effective for a young age group. Whilst the concept of shows at zoos may not be new, many have traditionally included performances by trained animals but Spooner et al. (2016) have shown that displays without animals can be effective, which could mean the end of using animals in such a controversial manner (Hosey et al., 2013 p.471).

The educational measures discussed so far have focused on young people and their families. Whilst groups with children may form the majority of zoo visitors (81.7%; Morgan and Hodgkinson, 1999) they should not be the only demographic that are targeted by zoo education. Many zoos host one-off talks or events relating to research conducted at the zoo or about the conservation programmes they support. Similar events could be aimed at organisations such as the Women's Institute or University of the Third age, with the content of the talks being expanded upon to include more general zoological or conservation topics.

Several zoos have already targeted local businesses in order to host 'away days', which may focus on teaching the attendees about animal enrichment. During these 'away days', businesses will pay up to £79.95 per person (current price at Colchester Zoo) for their staff to visit the zoo where they can learn about animal welfare and enrichment through talks by zoo staff, after which the attendees are able to construct their own enrichment devices. These days have proved to be highly successful as the animals are provided with novel enrichment, the attendees learn about animal welfare and the events lead them to feel empathy towards the specific animals receiving the enrichment, which often results in future monetary or physical donations (Kingston-Jones, 2014).

Regardless of the form of education that is used it is imperative to consider how educational messages are framed. When discussing conservation issues and ways in which visitors can change their behaviour, such as buying paper products with the FSC logo to alleviate deforestation, these messages can be framed positively or negatively. Positively framed messages highlight the benefits to the individual of performing such an action whilst negatively framed messages focus on the costs to the individual of not performing an action (Meyerowitz and Chaiken, 1987). A study encouraging young women to perform breast self-examinations found that negatively framed information has a stronger impact and individuals were more likely to change their judgement or behaviour than if similar, positively framed information was given (Meyerowitz and Chaiken, 1987). Message framing is a concept that has been considered when attempting to garner public behaviour changes relating to environmental issues, such as recycling and energy use, but has so far not been examined with regards to zoo education. On the topic of recycling, it was found that negatively framed messages, describing the problems that will occur if people do not act, worked well with young and well-educated individuals (Davis, 1995) and that communications related to environmental messages should target small and homologous groups rather than larger, diverse groups of people (Grunig, 1989). Unfortunately, zoo visitors are very demographically diverse, which may make communicating environmental messages more complicated. This suggests that research into message framing needs to be conducted in zoos to identify optimum methods of framing messages to lead to behaviour change. With this research it should also be noted that even if an educational message can be delivered to an individual, if this message is in opposition to their current viewpoint, attitude change is very difficult to achieve when individuals have pre-existing opinions (Cartwright, 1949), as discussed in chapter 6 If attitude change does not happen then behaviour change is also unlikely to occur. The topics of message framing and confirmation bias appear to be lacking in zoo education research and whilst current research in these areas suggest that being able to educate and obtain behavioural change from zoo visitors may be challenging understanding these issues and how they affect zoo education should lead to solutions.

So far I have discussed how zoos can educate the public but have not yet focused on what they should be trying to convey through such education. The results of study 1 in chapter 6 show that the surveyed visitors to Edinburgh Zoo were already aware of several basic facts about chimpanzees. For example 87% of all participants knew that humans and chimpanzees share more than 90% of their DNA. If general zoo visitors are already aware of the basic facts about zoo animal species, perhaps educators should try to include some more unusual or exciting facts that the public are unlikely to have heard before and they may remember. For example, humans and chimpanzees are so similar that they have the same blood types, meaning that a human can receive a blood transfusion from a chimpanzee (Ségurel et al., 2012). Alternatively, the content of all forms of education (talks, signs etc.) could have an overall theme. One interviewee mentioned that during the run up to the British General election in May 2015, they gave all of their ‘Keeper Talks’ a political theme in the hope of increasing visitor engagement. This idea could be taken further and combined with the above proposal to use unusual and exciting facts. ‘Deadly 60’ is a BBC children’s natural history series that began in 2009 with Steve Backshall travelling around the world to create a list of the 60 most ‘deadly’ species on the planet. The series was so successful it is now into its fourth season and been broadcast in 157 countries worldwide. Zoos could use a similar concept, possibly similar to ‘Top Trumps’ cards, where different aspects of species’ biology and behaviour could be compared easily.

On a more specific level, the results of study 1 in chapter 6 also highlight that zoo visitors still believe that natural looking enclosures, as well as enrichment, is important and that listening to the extended talk did not affect this belief. As mentioned previously, enclosures that look natural may be preferred by the public but the welfare of the animals that inhabit them is not necessarily good (Seidensticker and Doherty, 1996). It is vital that zoos aim to show the public that enclosures do not have to be naturalistic in appearance to support good welfare. By combining naturalistic layouts in visitor areas and artificial design inside enclosures, animal welfare is less likely to suffer from attempts to ensure enclosures fit with the desired style of the development. For example, in July 2015, Chester Zoo opened their immersive ‘Islands’ development. The area has been designed to simulate being on six different South-east Asian islands where visitors can observe animals endemic to each island. Whilst the area uses many plants and props to convey the idea of being in places like Bali and Sulawesi, many of the animal enclosures feature items that do not fit the natural aesthetic, such as poles and fire hose in primate enclosures. This design benefits not only the animals living within the enclosures but also the educational potential of the area.

Additionally, consulting the public themselves about what they want to be told about through zoo education may prove advantageous. One study carried out at Melbourne Zoo, Australia, asked visitors what kinds of conservation related behaviours they would be more likely to adopt (Smith et al., 2013). Visitors said they would be more likely to perform an action to benefit wildlife if it were possible to do so whilst still visiting the zoo and if that action was simple to implement. They also stated that they would be more likely to adopt behaviours that are likely to elicit a strongly positive outcome on the problem they are trying to solve. Finally, they specified they would prefer to undertake actions/behaviours they do not currently do or that are based on something new they have learnt at the zoo. A good example of a zoo conservation education scheme that adhered to these four statements is the project undertaken in Australian zoos to encourage visitors to recycle old mobile phones by handing out pre-paid postage bags to visitors in order to benefit gorillas by reducing the need for coltan mining (Zoos Victoria, 2009). The project is ongoing and has been hugely successful with 120,000 mobile phones being recycled through the project since 2008. This shows that despite many difficult challenges facing zoo educators it is possible for zoos to spread knowledge and empower members of the public to act positively for the benefit of wildlife.

Whilst it is vital to educate zoo visitors about animal species and conservation related behaviours they can engage in, zoos should also aim to increase awareness of the successful contribution they make to conservation projects (Thomas, 2016). Zoos and aquariums donate approximately $350 million each year to a wide variety of conservation projects (Barongi et al., 2015) and there are species, such as the Golden Lion-headed tamarin and West Indian rock iguanas (*Cyclura* spp; Grant and Hudson, 2014), that may not have survived without the contribution of zoos. If zoos are telling their visitors how to change their behaviour to benefit wild animal populations, those visitors need to trust that the zoos are also agents of positive change for wildlife.

In the future, zoos need to try new and innovative methods of education whilst also understanding and implementing ways to mitigate the difficulties involved in the issues surrounding educating diverse groups of the public. Much more research needs to be conducted on a regular basis to determine what knowledge zoo visitors currently have, how effective present forms of education actually are and how educational messages can be spread more effectively to ensure that the educational potential of zoos is fully realised.

<u>The future of Zoo-based Research</u>

For zoos to continue improving, for both the animals they house and the public that visit them, academics and zoo staff members will need to collaborate to conduct vital research. As I have demonstrated in this thesis, such collaborative research can be used to identify possible causes of animal anxiety, to assess the appropriateness of measures intended to improve animal welfare and highlight areas of visitor education and experiences that require more input. Academics and zoo staff are now working more closely together, identifying the contributions each group can make to the other and sharing information about how collaborative science aids zoos at events such as the BIAZA research symposium and Shape of Enrichment Regional or International Environmental Enrichment Conferences.

Zoo-based research will also be vital for shaping the public view of zoos in the future. In the past year, the social media storm at the death of the Western lowland gorilla Harambe at Cinncinati Zoo and the BBC Horizon documentary 'Should we close our Zoos?' have made the public debate about the future of zoos more visible than ever before. Closer public scrutiny of zoos allows zoos a platform to highlight the fantastic research that they are contributing to as well as incentivising them to make greater strides towards improvements.

One topic addressed during the Horizon documentary was that of the type of species housed in zoos. This is an area of vital importance to the future of zoos where research has and will continue to play a pivotal role. Whilst iconic charismatic megafauna, such as Elephants and Polar bears, have been a traditional part of many zoo collections, scientific studies of both captive and wild animals have suggested that many of these species experience very poor welfare in captivity (Clubb and Mason, 2002; Wechler, 1991). This has led some institutions to change their policy on certain species such as The Detroit Zoo who, in 2005, became the first zoo in America to stop keeping Elephants due to insufficient space and the cold Detroit climate being unsuitable for such a large Asian mammal. The zoo's Director has stated that more research is required into understanding the welfare of all individual animals within zoos so that their role in conservation for the benefit of wild animals is not at their own expense (Kagan, 2013). He has also advocated that zoos base decisions on collection planning from a view of individual animal quality of life over the quantity of species that they could house (Kagan et al., 2015). However, if zoos do follow this advice and limit the number of animals they accommodate they will have to either cope with the issue of surplus animals or putting animals on contraception. Whilst the latter option appears easier, research on Barbary macaques has shown that females on hormonal contraception behave significantly differently from other females not on contraception (Maijer and Semple, 2015), a phenomenon that may well also affect females of other species. Additionally, it is currently unknown if preventing females from breeding has an effect on their welfare. On the other hand, having surplus animals either results in having to provide space for animals that have no contribution to captive breeding programmes or culling (Lacy, 1995), a practice that has been used by zoos for many years but caused public uproar after the death of Marius the Reticulated giraffe at Copenhagen

Zoo in 2014. Public opinion may also affect whether or not zoos choose to follow the quality vs quantity line of argument. Whilst a large percentage of the public would welcome a change in the selection of animals available at zoos as an attempt to improve animal welfare, a recent study of visitors to Durrell Wildlife Park found the three types of animals visitors most wish to see when visiting zoos are elephants, big cats and monkeys (Carr, 2016).

Zoo collection planning will require copious amounts of research to ensure that any decisions made are in the best interest of the animals they currently house but equally will not alienate visitors, upon whom zoos rely for financial support. Future research into refining methods of animal welfare assessment, identifying sources of anxiety/stress, designing enclosures that maximise education value whilst promoting good welfare and how to successfully educate the public to understand the importance behind why their local zoo no longer has elephants, will need to be undertaken to ensure the successful continuation of 'the modern zoo'.

Conclusion

The first zoos opened to the public just under 200 years ago. For these institutions to continue to operate for the next 200 years they will need to continue striving for best practice, which can only be aided by conducting sound scientific research. From the research I have conducted, my suggestion would be for zoos to focus on improvements to animal welfare through 'preventative' approaches to enrichment in order to avoid behavioural issues developing and being selective in the species that they housed based on the needs of the animals. Zoos must also ensure that they are considered to be innovative places of learning through multiple evidence-based forms of education as well as being trusted by the public for providing good animal welfare and acting positively for conservation.

Recommendations for Zoo Professionals

- Based on the results of chapter 3, I recommend that zoos that house chimpanzees should consider the use of signs or volunteers/staff members to ask visitors to refrain from using flash photography and to avoid letting children scream. Also, the use of automatic/programmable 'feedpods' could reduce the length of time between feeding events, reducing yawning and associated anxiety.

- Chapter 3 also highlights that enclosure design and living as part of a socially complex group can help with the reduction of R/R in zoo-housed chimpanzees. I would therefore recommend that any new enclosures built for chimpanzees are done so with multiple areas, allowing the natural fission-fusion social system to be expressed by the animals within the enclosure.
- The results of both chapters 4 and 5 show that whilst music is not a form of stimuli that chimpanzees react negatively towards, it is not providing any positive enriching effects. As such, I recommend that zoos do not play music as a form of enrichment for chimpanzees and look for other methods of enriching those animals. If an institution plays music for keeper enjoyment, I would recommend that the keepers select music with less than 90 BPM and ensure that the animals always have the option to avoid hearing the music.
- Based on the results of chapter 6, I recommend that zoos undertake further research into how to improve the ability of 'Keeper Talks' to increase visitor knowledge on topics such as whether enrichment and enclosures need to look natural to be good for animal welfare. I suggest that more time and resources are allocated for undertaking evaluations into visitor knowledge to ensure talks are pitched appropriately and into the various potential impacts of 'Keeper Talk' using a variety of rigorous empirical assessment measures. Additionally zoos should avoid solely relying on social media as a method of feedback as it is likely to focus evaluation of keeper talks against the goals of visitor enjoyment, whilst neglecting their potentially important educational role.

Appendices

Appendix 1

Speaker insider insulated box, as used for studies 1 and 2 in chapter 4.

Appendix 2

Music used in studies 1 and 2 of chapter 4 and study 2 of chapter 5. * indicates music that was not included in study 2 of chapter 5.

Classical Title (Beats per minute)	Composer/Performed by (Duration mins:seconds)	Pop/rock Title (Beats per minute)	Artist (Duration mins:seconds)
Serenade in B Flat, Gran Partita – Adagio (68)	Mozart/Academy of St Martin in the Fields, conducted by Sir Neville Marriner (5:31)	Too Close (128)	Alex Clare (3:44)
Brandenburg Concerto #2 In G, BWV 1048 - 2. Andante (62)	JS Bach/Chamber Orchestra of Europe (3:21)	Rollin' in the Deep (100)	Adele (3:48)
Nocturne for piano No. 16 in E flat major, Op. 55/2, B. 152/2 (66)	Chopin/Daniel Barenboim (3:23)	Locked out of Heaven (144)	Bruno Mars (3:54)
BGN (46)	Elgar/ (2:42)	Troublemaker (108)	Olly Murs ft Flo Rida (3:06)
Clarinet Concerto in A - Adagio (84)	Mozart/Emma Johnson and the Royal Philharmonic Orchestra (7:31)	One More Night (95)	Maroon 5 (3:40)
Maid with the Flaxen Hair (66)	Richard Stoltzman/Slovak Radio Symphony Orchestra (2:49)	ET (92)	Katy Perry ft Kanye West (3:51)
Piano Sonata No 14 in C sharp minor Op 27 No 2 Moonlight - Adagio sostenuto (52)	Beethoven/ (5:07)	Beauty and a Beat (132)	Justin Beiber ft Nicki Minaj (3:48)
		We are Young (120)	*Fun ft Janelle Monáe (4:11)

Appendix 3

Time of when instantaneous scans were taken relative to the start time of the experimental session

Time of scans relative to start time (mins)	Time of scans relative to start time (mins)
0	31
3	34
6	37
9	40
12	43
15	46
18	49
21	52
24	55
27	58
29	60

Appendix 4

Mean observation times for three focal individuals during study 2 of chapter 4

Focal Individual	First Silence Control Mean in mins (SD)	Music Mean in mins (SD)	Second Silence Control Mean in mins (SD)
Lianne	29.40 (4.95)	27.76 (5.55)	29.39 (1.20)
Paul	28.31 (2.64)	19.56 (10.90)	28.50 (5.00)
Rene	26.73 (4.37)	22.97 (10.13)	26.62 (7.01)

Appendix 5

Demographic information on four groups of Chimpanzees at National Centre for Chimpanzee care

Name	Group	Gender	Age at Start of Study	Rearing
Hannah	C2	F	15	Mother
Coco	C2	F	21	Mother
June	C2	F	40	Unknown
Mae	C2	F	41	Unknown
Rhoda	C2	M	43	Unknown
Chester	C2	M	10	Mother
Rusty	C2	M	10	Mother
Austin	C2	M	14	Mother
Marcus	C2	M	14	Mother
Cordova	C2	M	34	Unknown
Gremlin	C2	M	35	Unknown
Pacer	C2	M	35	Unknown
Cassie	C4	F	17	Mother
Emily	C4	F	21	Mother
Lulu	C4	F	24	Mother
Abbey	C4	F	41	Unknown
Sandy	C4	F	44	Unknown
Lyle	C4	M	7	Mother
Tony	C4	M	16	Mother
Doyle	C4	M	23	Mother
Punch	C4	M	23	Mother
Kudzu	C4	M	23	Mother
Misty	C5	F	22	Mother
Helga	C5	F	40	Unknown
Ursula	C5	F	42	Unknown
Cody	C5	M	16	Mother
Joey	C5	M	34	Unknown
Zippy	C5	M	35	Unknown
Zoe	C8	F	4	Mother
Cecelia	C8	F	15	Mother
Tinker	C8	F	22	Mother
Kelley	C8	F	40	Unknown
Martha	C8	F	40	Unknown
Mary	C8	F	41	Unknown
Huey	C8	M	15	Mother
Pierre	C8	M	44	Unknown

Appendix 6

Music used in study 1 in chapter 5

Genre	CD Used – Title and Artist
Classical	25 Classical Favourites - Various composers
Rock	Best of 80's Metal, Vol. 1 - Various artists
African Folk	Dance My Children, Dance - Samite

Appendix 7

Transcript of extended chimpanzee 'Keeper Talk' as recorded on 22nd Feb 2015

Hello everyone, as Barry says, I'm doing a PhD here with the chimpanzees here at Edinburgh Zoo. The research I'm currently doing is looking into the ways of improving the welfare of captive chimpanzees using different types of enrichment, which keeps them physically and mentally stimulated. The keepers here use a lot of different types of enrichment, including scattering the food so the chimps have to get up and go to look for the food, as they would do out in the wild. They also fill plastic tubes with food, which the chimps have to think about how they will get the food out. Sometimes they will go and get sticks and they use them as a tool as they would do in the wild, which is fantastic. So these really unnatural looking items can be promoting natural type behaviours in the chimps.

The research that I'm doing is actually looking to see if music is a good form of enrichment. A lot of zoos do play music for chimps as they think that we [humans] like music, chimps are very similar to us so maybe they like it as well. So, I've been asking the chimps if they like music or not. Down in the research pods here in Budongo Trail we have a touchscreen, which is a little bit like an ipad, but protected so the chimps can't break it as they do enjoy breaking things! I used this to basically create a 'Jukebox'. So, there are three buttons; one turns music off, one turns on Classical music and one turns on Pop music. And I got the chimps to come and choose what they wanted to listen to. When we were training the chimps we would give them a grape to reward them for taking part and they really seem to love using the touchscreen. Even when we have finished a session with an individual they will carry on pressing the screen as if they want to carry on! So using the touchscreen in itself as a really good form of enrichment for the chimps as it is something they enjoy and it gets them to use their brains. It's a bit like us doing a Su Doku on an i-pad.

So, from our research we have found out that the Edinburgh chimps don't particularly like music. They don't seem to hate it but equally they aren't choosing to listen to it, so we don't really think that music is a very good form of enrichment.

Now, another part of my research is asking people's views of enrichment so I would be incredibly grateful if any of you would like to head over this way and fill out a quick questionnaire. It shouldn't take more than a few minutes and it will really help my research. Thanks very much.

Appendix 8

Questionnaire given to zoo visitor participants for study 1 of chapter 6

Gender: Male / Female Age_________ [Participant Number___________________ (Extended: Y/N)]

1) What do you think the environment of a captive animal should provide? (please tick all that apply)

a)Something that makes them use their brain		**b) A natural appearance that looks similar to habitat in the wild**	
c) The ability to perform behaviours they would do in the wild		**d)Something to lead to a reduction in abnormal behaviours**	
e) Opportunity to interact with visitors		**f) Allowing them to be active**	
g) Constant visibility of animals to the public			

2) (On a scale of 1 to 7) Do you think that doing tasks on a computer touchscreen is an effective form of enrichment for CHIMPANZEES?

Not at all 1 2 3 4 5 6 7 Extremely

3) (On a scale of 1 to 7) Do you think that scatter feeding (spreading out food so the animal has to search for it) is an effective form of enrichment for CHIMPANZEES?

Not at all 1 2 3 4 5 6 7 Extremely

4) (On a scale of 1 to 7) Do you think that it is important to keep CHIMPANZEES in naturalistic social groups?

Not at all 1 2 3 4 5 6 7 Extremely

5) (On a scale of 1 to 7) Do you think that listening to music is an effective form of enrichment for CHIMPANZEES?

Not at all 1 2 3 4 5 6 7 Extremely

6) (On a scale of 1 to 7) Do you think that having set meal times is an effective form of enrichment for CHIMPANZEES?

Not at all 1 2 3 4 5 6 7 Extremely

7) (On a scale of 1 to 7) Do you think that hearing visitors knocking on glass is an effective form of enrichment for CHIMPANZEES?

Not at all 1 2 3 4 5 6 7 Extremely

8) How much DNA (genetic material) do we share with Chimpanzees? More than 90% less than 90%

9) (On a scale of 1 to 7) How similar do you think the mind and behaviour of humans and chimpanzees are?

Extremely 1 2 3 4 5 6 7 Not at all

10) (On a scale of 1 to 7) How important are the following when designing captive conditions for chimpanzees?

a) Make the enclosure look as similar to the animal's natural habitat as possible

Not at all 1 2 3 4 5 6 7 Extremely

b) Ensure that they are allowed to express natural behaviours

Not at all 1 2 3 4 5 6 7 Extremely

c) Ensure that the animals are always visible to visitors

Not at all 1 2 3 4 5 6 7 Extremely

d) Enrichment is similar to something the animals would experience in the wild

Not at all 1 2 3 4 5 6 7 Extremely

e) Engage them in activities that require them to think

Not at all 1 2 3 4 5 6 7 Extremely

11) What is the highest level of Education you've completed:

Primary School GCSE A-Level Degree Postgraduate Other (please specify)

12) In the past year, how many times did you visit a zoo, including today's visit? 1 2-3 4-5 6-10 10+

13) Are you a vegetarian? Yes No

14) Do you own any of the following animals? (please circle all that apply) Dog Cat Rabbit/Guinea pig Hamster/rat/gerbil/mouse Lizard/snake/tortoise Fish Horse Birds Other______________________

15) Are you a member of or do you donate to any of these animal welfare charities? (please circle all that apply)

SPCA/RSPCA Blue Cross The Brooke Born Free PETA World Animal Protection Other______________________

<u>Appendix 9</u>

Questionnaire for zoo professionals in study 2 of chapter 6

Participant Number _________ Job Title_________________________ Institution ______________________

Do you have chimpanzees at your institution? Y / N

Imagine 100 of your visitors who have visited your chimpanzee enclosure but have not attended a 'Keeper talk' were asked the questions below that relate to effective enrichment for chimpanzees. Please circle the percentage of those people you estimate would get the answer correct. (Answers considered correct are underlined)

1. Do humans and chimps share more or less than 90% of our DNA?
Answer: <u>More</u> Less
What percentage got this right? 0-10 10-20 20-30 30-40 40-50 50-60 60-70 70-80 80-90 90-100
2. How similar do you think the mind and behaviour of humans and chimpanzees are?
Extremely <u>1 2 3</u> 4 5 6 7 Not at all
What percentage got this right? 0-10 10-20 20-30 30-40 40-50 50-60 60-70 70-80 80-90 90-100
3. Is knocking on windows a good form of Enrichment?
Not at all <u>1 2 3</u> 4 5 6 7 Extremely
What percentage got this right? 0-10 10-20 20-30 30-40 40-50 50-60 60-70 70-80 80-90 90-100
4. Are touchscreens good Enrichment?
Not at all 1 2 3 4 <u>5 6 7</u> Extremely
What percentage got this right? 0-10 10-20 20-30 30-40 40-50 50-60 60-70 70-80 80-90 90-100

5. How important is it to make the enclosure look as similar to the animal's natural habitat as possible?
Not at all 1 2 3 4 5 6 7 Extremely
What percentage got this right? 0-10 10-20 20-30 30-40 40-50 50-60 60-70 70-80 80-90 90-100
6. How important is it to ensure that the animals are allowed to express natural behaviours?
Not at all 1 2 3 4 5 6 7 Extremely
What percentage got this right? 0-10 10-20 20-30 30-40 40-50 50-60 60-70 70-80 80-90 90-100
7. How important is it to ensure that the animals are always visible to visitors?
Not at all 1 2 3 4 5 6 7 Extremely
What percentage got this right? 0-10 10-20 20-30 30-40 40-50 50-60 60-70 70-80 80-90 90-100
8. How important is it for Enrichment is similar to something the animals would experience in the wild?
Not at all 1 2 3 4 5 6 7 Extremely
What percentage got this right? 0-10 10-20 20-30 30-40 40-50 50-60 60-70 70-80 80-90 90-100
9. How important is it to engage the animals in activities that require them to think?
Not at all 1 2 3 4 5 6 7 Extremely
What percentage got this right? 0-10 10-20 20-30 30-40 40-50 50-60 60-70 70-80 80-90 90-100
10. Is music a good form of Environmental Enrichment?
Not at all 1 2 3 4 5 6 7 Extremely
What percentage got this right? 0-10 10-20 20-30 30-40 40-50 50-60 60-70 70-80 80-90 90-100

Appendix 10

Basic questions asked during the semi-structured interviews in study 2 for chapter 6, along with initial suggestions for answers

- What is the target audience of your talks? E.g. age, educational/knowledge level etc.
- What is the main aim of these talks?
    - Consolidate existing Knowledge
    - Present new information
    - Create empathy towards the animals
- Do you have a standardised content of ‘keeper talks’?
- How often do you change the material included in your talks or the types of talks given?
- What informs these changes?
    - Scientific studies
    - Comments from Visitors
    - Research on visitor knowledge
- How do you assess the impact of your talks?
    - Comments from Visitors
    - Research on visitor knowledge
    - TripAdvisor reviews
- Do you ever investigate the existing knowledge of your visitors?

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