

AN ASSESSMENT OF THE DEVELOPMENT
OF A COGNITIVE RESEARCH PROGRAMME
AND INTRODUCTIONS IN ZOO-HOUSED
CHIMPANZEES

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For Claire Gresswell:

An amazing friend and dedicated conservationist whose strength, optimism, and humour in the face of adversity were insurmountable.



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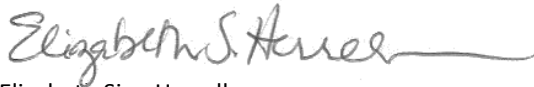
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DECLARATION

I declare that the work undertaken and reported within this thesis is my own and has not been submitted in consideration of any other degree or award.



Elizabeth Sian Herrelko

PUBLICATIONS, PRESENTATIONS, AND MEDIA

The following publications, presentations, and media have been adapted from work detailed in this thesis:

PUBLICATIONS

Herrelko, E.S. (2009). Book Review: *Observing animal behaviour: Design and analysis of quantitative data* by Marian Stamp Dawkins. *Primate Eye* 98, 48-49.

Herrelko, E.S., Vick, S.J., & Buchanan-Smith, H.M. (under review). Cognitive research in zoo-housed chimpanzees: Influence of personality and impact on welfare

Herrelko, E.S., Vick, S.J., & Buchanan-Smith, H.M. (in prep). Can video introductions and personality profiles predict chimpanzee introduction outcomes?

Herrelko, E.S., Vick, S.J., & Buchanan-Smith, H.M. (in prep). Welfare implications of chimpanzee introductions.

Herrelko, E.S., Vick, S.J., & Buchanan-Smith, H.M. (in prep). The Chimpcam Project: Assessing public engagement with science.

PRESENTATIONS

Ethical considerations in chimpanzee research: Animal welfare and public perception. 13th Annual BIAZA Research Symposium. Bristol Zoo, Bristol, England. 6 July 2011.

Snog, Marry, Avoid? Chimpanzee introductions. Behaviour and Evolution Research Group. University of Stirling, Stirling, Scotland. 2 March 2011.

The Chimpcam Project: Training chimpanzees to use touchscreens. Department of Psychology Seminar Series. University of Portsmouth, Portsmouth, England. 2 February 2011.

Lights, chimpcam, action: A multi-organisational partnership with a zoo, university, and wildlife filmmakers. The Burn, Scottish Primate Research Group. Glenesk, Angus, Scotland. 22 January 2011.

Assessing welfare: A new cognitive research programme for the chimpanzees (Pan troglodytes) of Budongo Trail, RZSS. Behaviour and Evolution Research Group. University of Stirling, Stirling, Scotland. 29 September 2010.

Assessing welfare: A new cognitive research programme for the chimpanzees (Pan troglodytes) of Budongo Trail, RZSS. International Primatological Society XXIII Congress. Kyoto University, Kyoto, Japan. 15 September 2010.

Lights, camera, action: A multi-organisational partnership with a zoo, university, and wildlife filmmakers. 12th Annual BIAZA Research Symposium. Chester Zoo, Chester, England. 8 July 2010.

Training chimpanzees for touch screen tasks. Primate Society of Great Britain Spring Meeting Pre-conference Cognition Workshop. Royal Zoological Society of Scotland, Edinburgh, Scotland. 6 April 2010.

The Chimpcam Project: An overview. The Burn, Scottish Primate Research Group. Glenesk, Angus, Scotland. 17 January 2010.

The Chimpcam Project. Budongo Centenary Evening. Royal Zoological Society of Scotland, Edinburgh, Scotland. 9 December 2009.

Is training for cognitive testing stressful? A comparison of self-directed behaviours of chimpanzees (Pan troglodytes). Primate Society of Great Britain Winter Meeting. Zoological Society of London, London, England. 2 December 2009.

The Chimpcam Project. Royal Zoological Society of Scotland Education Class. Edinburgh, Scotland. 10 November 2009.

Is training for cognitive testing stressful? A comparison of self-directed behaviours of chimpanzees (Pan troglodytes). Behaviour and Evolution Research Group. University of Stirling, Stirling, Scotland. 13 October 2009.

Training for cognitive testing as a method of enrichment in Budongo Trail, the Royal Zoological Society of Scotland (RZSS). International Conference on Environmental Enrichment. Torquay, England. 2 June 2009.

Training chimpanzees for cognitive testing at Budongo Trail, Royal Zoological Society of Scotland. Scotland Conference on Animal Behaviour. Glasgow, Scotland. 18 April 2009. (Poster)

An exploration of self-recognition in captive chimpanzees (Pan troglodytes). Behaviour and Evolution Research Group. University of Stirling, Stirling, Scotland. 20 September 2008.

Chimpcam Project – an examination of chimpanzee (Pan troglodytes) cognition. Postgraduate Presentation Day. University of Stirling, Stirling, Scotland. 20 June 2008.

MEDIA

Natural World: The Chimpcam Project (2010)¹

- Networks: BBC and Animal Planet
- Role: Presenter/major contributor
- Content: Documentary based on first 18 months of this project
- Press: Numerous international interviews for television, radio, newspapers, and magazines

The Origins of Us (2011)

- Network: BBC
- Role: Contributor (Episode 3, “Brains”)
- Content: Three-minute segment highlighting group interactions following chimpanzee introductions

¹ A DVD of the Chimpcam Project is attached to the back cover of this book.

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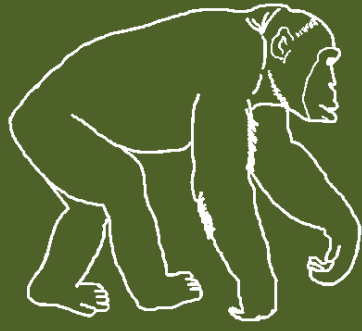
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ABSTRACT

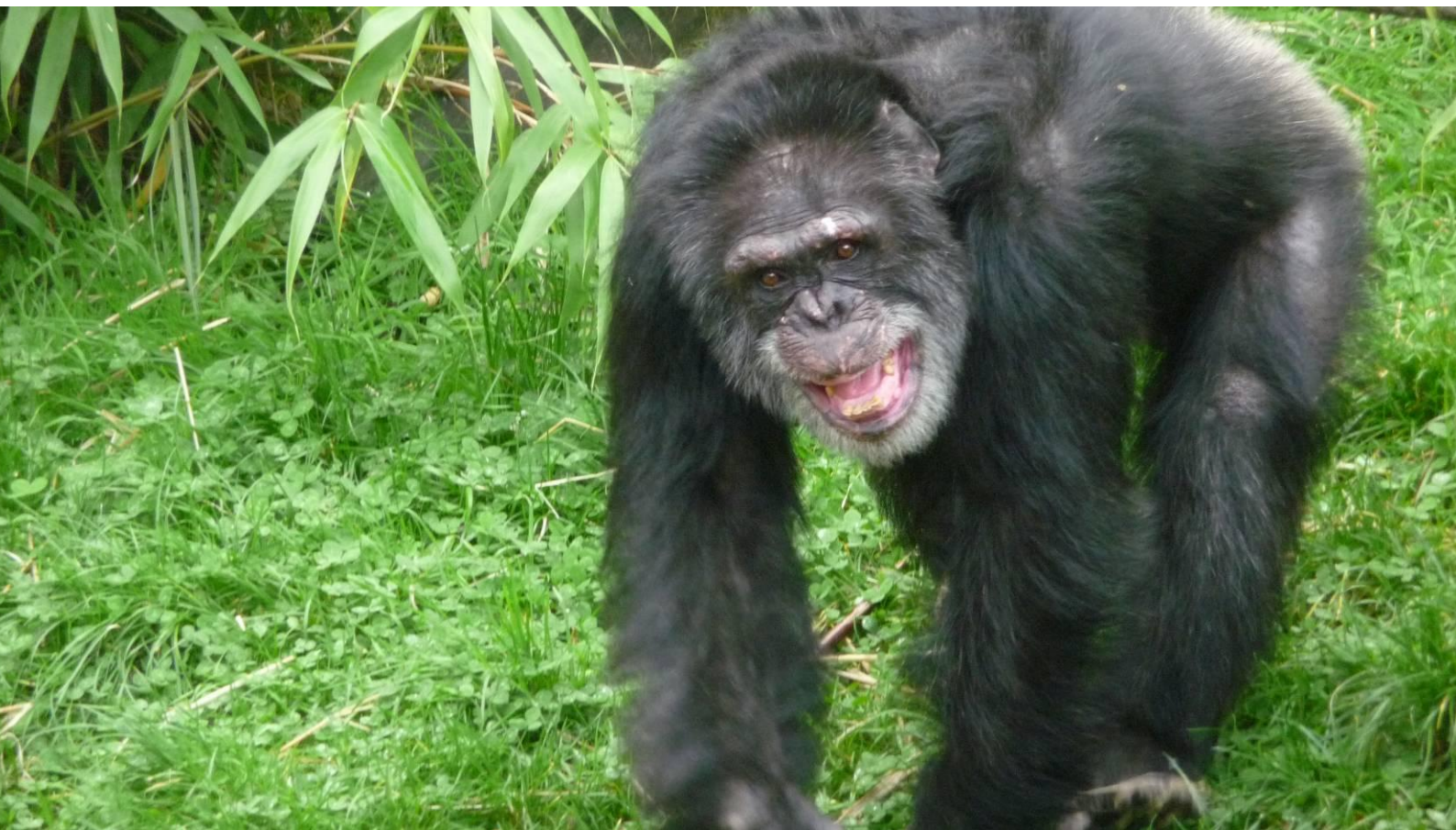
Zoological institutions emphasise the importance of excelling in the areas of animal welfare, conservation, education, and research, not only to better the lives of the animals under their care, but to also influence the general population in the pursuit to conserve the natural world. As a result, zoo life is anything but simple. This research project monitored the lives of a captive group of chimpanzees over a two-and-a-half-year period, during which time we explored four research topics while assessing the development of a cognitive research programme and chimpanzee (*Pan troglodytes*) introductions in a zoo: welfare, cognition, public engagement with science, and animal management. The project's use of touchscreen technology and on-exhibit research was the first of its kind for the Royal Zoological Society of Scotland's Edinburgh Zoo. As a result, the researchers placed a great deal of importance not only on assessing the welfare of the chimpanzees throughout training and testing phases, but also assessing the public's perception of cognitive research being conducted through an internationally broadcast documentary about the project. In the short duration of the project, these research naïve chimpanzees did not fully grasp the concept of video selection in our free-choice activity, but overall, the introduction of a cognitive research programme did not compromise welfare, and the chimpanzees' repeated interest suggests that chimpanzees found the research to be reinforcing. Partly funded by the BBC, the Chimpcam Project was shown in the UK (broadcast January 2010) and in a variety of other countries, including the United States and Canada (on Animal Planet in 2011). The broadcast allowed us to gather information over the internet on the wider public's perception of conducting research with great apes in zoos, to complement data collected on visitors to the exhibit itself. Our assessment of the documentary's impact on public perception showed that it had a positive influence on perceptions of zoo research, scientists, welfare, and the importance of choice for animals. During this research project, a new group of chimpanzees arrived in Edinburgh as part of the international breeding programme for western chimpanzees (*Pan troglodytes verus*). As the zoo's focus switched to helping the two chimpanzee groups merge into one, we took the opportunity to apply psychological research to this context, namely the use of video as a research tool and the recognition of the importance of individual differences in response to challenge. The project maintained the cognition and welfare focus by using video introductions (allowing the chimpanzees to watch video footage of the individuals they were

about to meet and track the formation of other sub-groups). In addition, personality ratings and chimpanzee behaviour during the visual access period (an animal management technique used prior to physical introductions where the groups could see each other without physical contact) were collected to examine the efficacy of these measures in guiding introductions in order to reduce risk. Personality ratings and behaviours observed during the video introductions could predict the chimpanzees' behaviour during the physical introductions, however, the visual access period had no predictive power. The welfare implications of the introduction process were also assessed and suggested that: the choice of location (i.e. options of where to be) was more important than the total amount of available space; having individuals removed from your group was more stressful than having individuals added; self-directed behaviour (SDB) performance was context-specific where rubbing significantly increased during periods of uncertainty that were not necessarily negatively valenced; regurgitation and reingestion (R/R) decreased over time; and both in-group members and those of high ranks spent more time grooming others. Overall our data indicate that the chimpanzees coped well with both cognitive challenges and social upheaval during introductions. Despite being regularly studied in captivity and in the wild, chimpanzees have a great deal more to teach us about their world. In order to provide the best welfare for the chimpanzees in our care, we need to understand how research and management practices affect their lives and how the public interpret what we do as researchers. By understanding these aspects of their world, we can better serve those in captivity and influence public opinion on the importance of conserving those in the wild.



CHAPTER 1

GENERAL INTRODUCTION



GENERAL INTRODUCTION

1.1 RESPONSIBILITIES OF A ZOO

The responsibilities of zoos to animals (under their care as well as in the wild) and humans are extensive. As a member of a professional zoological organisation, such as the British and Irish Association of Zoos and Aquariums (BIAZA), a zoo must not only adhere to legislation within their own country (e.g. for the UK: the Zoo Licensing Act 1981 (Amendment) (England and Wales) Regulations, 2002 and the Secretary of State's Standards of Modern Zoo Practice, 2000), but also excel in four main areas: animal welfare, conservation, education, and research (BIAZA, 2009a). As ambassadors for their wild counterparts (Bertram, 2004), zoo animals inspire us to research them to learn more about how we can best conserve the wild, tend to those under our care, and educate the public in the hopes that they will join the world-wide effort to conserve species. When working within a zoo for research or other purposes, each of these areas inevitably play a role, which can result in a holistic approach to working with animals. The following pages address these areas within the context of the lives of the Budongo Trail chimpanzees (for details, see Section 2.2), from May 2008 through October 2010, as they experienced the development of a cognitive research programme and the introduction of 11 unfamiliar chimpanzees to their group.

1.2 CHIMPANZEES (*PAN TROGLODYTES*)

Chimpanzees, our closest living relatives, inform our understanding of how evolution has shaped human behaviour and cognition; a concept that plays an important role in the ongoing improvement of captive care and conservation. Chimpanzees are relatively adaptable primates that live in a variety of habitats across equatorial Africa (Goodall, 1986). In the wild, they live in social communities of up to one hundred individuals and regularly practice fission-fusion (Nishida, 1979) by breaking apart into smaller social groups or parties within their dynamic society (Aureli et al., 2008). Within these communities, males dominate over females and are ranked within a linear dominance hierarchy (Nishida, 1979) where individuals earn high-ranking positions through a combination of physical strength and social intelligence (Goodall, 1986).

As intelligent animals, chimpanzees are known for their abilities to work cooperatively with each other (Boesch, 1994), plan for the future (Osvath, 2009), recognise their own reflections (Gallup, 1970), empathise (Povinelli et al., 1992), emulate (Tomasello et al., 1987), imitate (Whiten et al., 1996), understand numbers (Matsuzawa, 1985), use mental maps (Boesch & Boesch, 1984), tools (Goodall, 1986; Sanz & Morgan, 2009), and deception (Byrne & Whiten, 1992) to their own benefit. They are curious beings with an interest in exploring novel items (e.g. using a stick to investigate a hidden camera; Morgan & Sanz, 2010). These qualities combined with their occasionally volatile social relationships, not unlike humans, make them fascinating to study and help make our findings easily digestible to general audiences.

1.2.1 POPULATION STATUS IN THE WILD AND IN CAPTIVITY

The International Union for Conservation of Nature (IUCN) Red List has classified chimpanzees as being an endangered species since 1996 (Oates et al., 2008). Even though chimpanzees are widespread throughout Africa, with an approximate population of 172,700 to 299,700 chimpanzees (Butynski, 2003), their endangered status is justified based on a sharp decrease in habitat and population over more than the past 20 years (Boesch & Boesch-Achermann, 2000). For each of the four subspecies (*P.t.elliotti*, *P.t.schweinfurthii*, *P.t.troglodytes*, and *P.t.verus*), the numbers are even smaller with *P.t.verus* (21,300 – 55,600) and *P.t.elliotti* (less than 6,500) being least represented (Oates et al., 2008).

According to animal management records, there were 678 chimpanzees (regardless of subspecies) housed in captivity within Europe in 2009, and of those, 207 were known to be the subspecies *P.t.verus* (Carlsen, 2009). With 22 individuals included in these studies, including nine *P.t.verus*, 3.24% of the European population of *Pan troglodytes* and 4.35% of *P.t.verus* were represented in this thesis.

1.2.2 CAPTIVE POPULATION MANAGEMENT

Population management for captive animals is planned in great detail by international organisations with the goal of maintaining healthy populations over time (EAZA, 2011a) where 90% of genetic diversity is sustained over 100 years (Frankham et al., 2002). The Royal Zoological Society of Scotland's (RZSS) Edinburgh Zoo is a member of the World Association of Zoos and Aquariums (WAZA), the

European Association of Zoos and Aquaria (EAZA), and the British and Irish Association for Zoos and Aquariums (BIAZA); three organisations that promote high standards and practices in the zoo community and facilitate and encourage cooperation (e.g. animal transfers) amongst zoos. The chimpanzees at Edinburgh Zoo, along with all chimpanzees in EAZA institutions, are organised by a European Endangered species Programme (EEP) coordinator and a European Studbook (ESB) keeper for their species. Studbook keepers collect and organise all of the population data (births, deaths, transfers, etc.) in order to make breeding or relocation recommendations (EAZA, 2011b).

As the need to increase the *P.t.verus* (commonly known as western chimpanzees) population was recognised by EAZA, DNA tests were carried out to establish the lineage and subspecies of each chimpanzee in EAZA collections (D. McGarry, personal communication, 2009). Edinburgh Zoo housed 11 chimpanzees, only two of which were *P.t.verus* (both males), in a newly built enclosure that could house up to 40 individuals. After several years of planning, a suitable group of 11 chimpanzees from Safaripark Beekse Bergen (the Netherlands) were transferred to Scotland on 18 March 2010 to merge with the established group of 11 chimpanzees in Edinburgh Zoo. Out of the 22 individuals, seven had permission to breed (i.e. *P.t.verus* and unrelated to the other group members); two males and three females from the Beekse Bergen group and two males from the Edinburgh group.

1.3 RESEARCH PROGRAMMES IN ZOOLOGICAL INSTITUTIONS

Over the years, accredited zoological institutions have transitioned from primarily being entertainment-oriented facilities to conservation organisations and platforms for public engagement with science (Kisling, 2001; Zimmerman et al., 2009). In 2008, EAZA published a research strategy encouraging zoos to develop and support a scientific culture enabling collaborations within and across institutions both *in* and *ex situ* (Reid et al., 2008). By incorporating research into mission statements and daily activities, zoos have developed additional ways to support their conservation goals (e.g. RZSS's support of the Budongo Conservation Field Station in Uganda) and further their expertise in animal management (e.g. using positive reinforcement techniques to increase welfare; Pomerantz & Terkel, 2009).

In the past, zoo research primarily focused on animal welfare, conservation, populations, and veterinary medicine (Thompson, 1993), but in recent years, there has been an increasing interest in exploring the

animal mind (also known as cognitive research) through non-invasive, interactive, and observational research. A number of zoos have participated in cognitive research, for example: Wildlife Conservation Society's New York Aquarium (Reiss & Marino, 2001) and Bronx Zoo (Plotnik et al., 2010); National Zoo (Shumaker et al., 2001); Lincoln Park Zoo (Lonsdorf et al., 2009); Zoo Leipzig (Albiach-Serrano, 2010); Dolphin Research Centre (Jaakkola et al., 2010); Disney's® Animal Kingdom (Leighty et al., 2011); Zoo Atlanta (Perdue et al., 2011); Royal Zoological Society of Scotland's Edinburgh Zoo (Herrelko et al., under review). Given the international interest, it is likely that the trend will continue.

1.3.1 COGNITIVE RESEARCH PROGRAMMES IN ZOOLOGICAL INSTITUTIONS

Our interest in the animal mind, particularly great apes, has been long standing with the first book exploring animal intelligence dating back to the 19th century (Romanes, 1886). Cognitive research with great apes has been active for many years in laboratory settings (Yerkes, 1916; Yerkes & Yerkes, 1921; Köhler, 1925, cited in Maestriperi, 2003; Gallup, 1970; Rumbaugh et al., 1973; Matsuzawa, 1985; Menzel et al., 1985; Boysen & Berntson, 1989; Kawai & Matsuzawa, 2000; Parr, 2001; Poss & Rochat, 2003; Hirata, 2007), but for zoos, this is a relatively young science with more recent methods having origins in Markowitz's concept of engineering environments (1978) where enclosure designs aim to stimulate animals both mentally and physically. The Think Tank at the National Zoo, Washington DC was the first of its kind when Rob Shumaker took his research on public display in 1995 to offer zoo visitors a close up look at how cognitive research works and illustrate the intelligence of orangutans (Shumaker, 2002). Providing an opportunity for the public to watch research as it happens, allows visitors a unique peek into the animals' lives in an environment that aims to foster understanding and respect for the animal participants (see Chapter 5 for visitor perceptions of cognitive testing as seen through a documentary about research at RZSS's Edinburgh Zoo). Over a decade later, several zoos started to follow suit by creating research areas on public display: Zoo Leipzig (2001), Lincoln Park Zoo (2004), Zoo Atlanta (2007), RZSS's Edinburgh Zoo (2008), Kyoto City Zoo (2009), Marwell Zoo (2011), and Oregon Zoo (in development).

The addition of a cognitive research programme has the potential to be an exciting endeavour for many zoos. RZSS's mission statement is "to inspire and excite our visitors with the wonder of living animals

and so to promote the conservation of threatened species and habitats” (Royal Zoological Society of Scotland, 2010). By providing mentally stimulating activities for the animals, new training situations for the keepers, and outreach through publications and public engagement with science, the introduction of cognitive research to zoos can address the aims of their mission statements (e.g. Perdue et al., 2011). With zoos taking great pride in their husbandry and welfare standards to create socially and physically enriched environments to ensure psychological wellbeing, and having a varied collection with respectable sample sizes, zoos offer many benefits for scientific researchers (Kleiman, 1992).

1.3.2 CHALLENGES IN ZOO RESEARCH

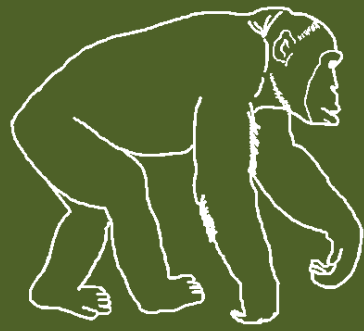
Scientists have faced many challenges during the nearly 30 years that formal zoo research programmes have been in practice (Wharton, 2007). One of the biggest struggles encountered when working in zoos is incorporating controlled methodology into daily management practices of zoo staff (Hosey, 1997; Wharton, 2007). Keeper time is a valuable commodity and adding a research time commitment into their already full schedule can be challenging. However with animal welfare, conservation, and public engagement with science being priorities for both zoo staff and researchers, research requests are often met with interest. Flexibility between management scheduling and research methodology can lead to successful collaborations.

1.4 THESIS AIMS

Opportunities to study research-naïve chimpanzees, chimpanzee introductions, and public engagement with science (PES) focused on an internationally broadcast documentary about the development of a cognitive research programme are rare events, reports of which are not well represented in the literature. With the addition of the new chimpanzee habitat, Budongo Trail at RZSS’s Edinburgh Zoo, an opportunity to study all three events surfaced. This thesis aims to evaluate the development of a cognitive research programme using a BBC documentary about the project as a public engagement tool and chimpanzee introductions in a zoo by focusing on four topics: welfare, cognition, public engagement with science, and animal management.

1.5 THESIS OUTLINE

The studies within this thesis are divided into two sections encompassing the development of a cognitive research programme and chimpanzee introductions. The first section includes three chapters: Chapter 3 assesses the performance of research naïve chimpanzees on their first cognitive activities. Chapter 4 provides a welfare assessment during the development of the cognitive research programme. Chapter 5 details an assessment of public engagement with science revolving around the development of the cognitive research programme using a wildlife documentary as a tool to inform an international audience about the trials and tribulations of research and to portray a real-life environment for animal research. The second section includes two chapters: Chapter 6 provides an account of the chimpanzee introduction process and examines the behavioural predictors of introduction outcomes. Chapter 7 describes the welfare implications of chimpanzee introductions in terms of self-directed and abnormal behaviours, the stages of the introduction process, changes in group size, space availability, and allogrooming. A general discussion in Chapter 8 links the studies together with a summary of the findings and provides recommendations for zoo professionals.



CHAPTER 2

GENERAL METHODS



GENERAL METHODS

2.1 INTRODUCTION

This thesis examines multiple topics: cognition and preferences in response to live-video feeds; welfare during the development of a cognitive research programme within an applied zoo context; public engagement with science, in terms of the impact of a documentary about the chimpanzees of Budongo Trail and their interest in cognitive research; behavioural predictors and welfare implications of chimpanzee introductions, including the novel use of video introduction and personality profile measures. While the overarching methodological approach is covered in this chapter, the methods of each study are covered in-depth in subsequent chapters.

While research is central to the aim of many zoos (EAZA, 2008), challenges inevitably arise when multiple aims conflict (e.g. research sessions may have to be put on hold due to enclosure maintenance; or an animal that is important to a research project might need to be transported to another institution because he/she is also genetically important to the breeding population). Regardless of the challenges, the benefits of working within a zoological institution can far outweigh the struggles that arise. For cognitive research, working in a zoological setting is ideal as it generally provides a more naturalistic setting than laboratories (e.g. social and environmental), making studies more ecologically valid, while providing better control over manipulations than in the field.

As captive animals need to be mentally stimulated for their psychological wellbeing, cognitive research can serve as a new and potentially enriching activity option in which the animals can choose to participate (Meehan & Mench, 2007; Yamanashi & Hayashi, 2011). Although providing activities would intuitively seem to be beneficial to welfare, it is possible that it may cause some undesirable stress or uncertainty to the animal (Leavens et al., 2001). For this reason, in addition to qualitative observations from staff, quantitative assessments are helpful to establish the implications of cognitive research on the animals' wellbeing. Assessing welfare during the onset of a cognitive research programme (Chapter 3) was designed to cover a 16-month period during which all cognitive training and testing (Chapter 4) was observed and coded for behaviours of interest.

The training and experiments carried out in Chapter 3 were developed to give the chimpanzees experience with the properties of video, in order to reach the goal of one of our funding bodies (Burning Gold Productions with BBC and Animal Planet), to provide the chimpanzees with a chimpanzee-proof video camera, called the Chimpcam, to see what they would do with it. All of these activities were the subject of a BBC Natural World and Animal Planet documentary, the Chimpcam Project. While the Chimpcam aspect of the project is not a highlighted study within this thesis, it was the motivating factor behind the project's design and inspired an additional study which assessed the impact of the documentary on the public's engagement with science (see Chapter 5).

Following the documentary, the number of chimpanzees housed in Budongo Trail doubled. With the acquisition of a second group from a park in the Netherlands, the number of chimpanzees rose dramatically, from 11 to 22 individuals. The chimpanzee introductions brought about a unique opportunity to use the training and cognitive video methods in an applied setting, video introductions between individuals and groups (Chapter 6), and continue the welfare assessments to examine the welfare implications of chimpanzee introductions (Chapter 7) using a similar methodology to the previous welfare study. The following sections outline the methods used within this project. Further details are described within each corresponding chapter.

2.2 PROJECT ANIMALS

Twenty-two chimpanzees (*Pan troglodytes*) from two groups housed in the Budongo Trail exhibit of RZSS's Edinburgh Zoo participated in these studies. The two groups were comprised of the Edinburgh group and the Beekse Bergen group (from Safaripark Beekse Bergen in the Netherlands). The Edinburgh group consisted of six male and five female chimpanzees ranging in age from 9 to 47 years (mean = 26.09; SE mean = 3.84) at the onset of the study (May 2008). The Beekse Bergen group consisted of five male and six female chimpanzees ranging in age from 13 to 41 (mean = 21.64; SE mean = 2.48) at the onset of their involvement in the study (March 2010). Demographic data for all individuals can be seen in Table 2.1 with dominance rank information in Table 2.2 and photographs in Figures 2.1 and 2.2.

Table 2.1. Participant information listed by date of birth.

House Name	Original Group	Arks #	Sex	Sire #	Dam #	Rear	DOB	Acquired by RZSS
Ricky	ED	660401	M	UNK	UNK	P	est. 1961	20.04.1966
Cindy	ED	710701	F	UNK	UNK	P	est. 1964	01.07.1971
Pearl	BB	M10C07	F	UNK	UNK	P	13.03.1969	18.3.2010
Lucy	ED	761101	F	UNK	681201	P	11.11.1976	11.11.1976
Louis	ED	820801	M	UNK	UNK	P	est. 1976	26.08.1982
David	ED	750301	M	670702	620601	P	02.02.1975	02.02.1975
Eva	BB	M10C11	F	Jacob	Victoria	H	09.12.1980	18.3.2010
Emma	ED	91DA01	F	L32	L29	P	15.08.1981	18.04.1991
Sophie	BB	M10C08	F	M66003	M67003	H	22.11.1981	18.3.2010
Lyndsey	ED	831201	F	750301	710701	P	24.12.1984	24.12.1984
Lianne	BB	M10C09	F	M66003	Yoko	P	14.02.1989	18.3.2010
Heleen	BB	M10C10	F	David	M81009	P	16.04.1991	18.3.2010
Qafzeh	ED	92CB04	M	UNK	91DA01	P	31.03.1992	31.03.1992
Kilimi	ED	93BB01	F	750301	831201	P	20.02.1993	20.02.1993
Rene	BB	M10C03	M	Billy	Agnetta	H	21.02.1993	18.3.2010
Bram	BB	M10C02	M	UNK	Yoko	H	27.03.1986	18.3.2010
Claus	BB	M10C04	M	M66003	M10C11	H	30.04.1993	18.3.2010
Paul	BB	M10C05	M	M66003	M70001	P	08.05.1993	18.3.2010
Frek	BB	M10C06	M	M66003	M68001	P	21.10.1993	18.3.2010
Edith	BB	M10C12	F	M66003	M10C11	P	11.04.1996	18.3.2010
Kindia	ED	97BB04	M	750301	831201	P	05.02.1997	05.02.1997
Liberius	ED	99AB04	M	780201	761101	P	20.01.1999	20.01.1999

Note: Sire/dam house names were provided when Arks numbers were not known. (Legend: BB = Beekse Bergen group; ED = Edinburgh group; M = Male; F = Female; UNK = Unknown; P = Parent reared; H = Hand reared; DOB = Date of birth; Est. = Estimated.)

Table 2.2 Dominance ranks for the Edinburgh and Beekse Bergen groups prior to the introduction process based on keeper and researcher assessment, in order of rank (sex listed in parentheses).

Rank	Edinburgh Group	Beekse Bergen Group
High	1 - Qafzeh (male)	1 - Claus (male)
	2 - David (male)	2 - Paul (male)
	3 - Louis (male)	3 - Eva (female)
	4 - Emma (female)	4 - Pearl (female)
Medium	5 - Kindia (male)	5 - Rene (male)
	6 - Lucy (female)	6 - Bram (male)
	7 - Liberius (male)	7 - Frek (male)
Low	8 - Kilimi (female)	8 - Edith (female)
	9 - Lyndsey (female)	9 - Heleen (female)
	10 - Ricky (male)	10 - Sophie (female)
	11 - Cindy (female)	11 - Lianne (female)

Note: See Section 2.4.3.2 for data collection methods of dominance ranks.

The two groups spent most of their lives in very different captive living situations. With the exception of three wild-caught individuals, the Edinburgh group were born and raised in typical zoo environments, whereas the Beekse Bergen group first moved into a zoo environment in 2007 (Safaripark Beekse Bergen, the Netherlands) after being relocated and formed into a social group made up of individuals retired from a biomedical laboratory (Biomedical Primate Research Centre, the Netherlands). The Beekse Bergen group moved to Edinburgh as part of EAZA's captive breeding programme for the West African subspecies of chimpanzee (*Pan troglodytes verus*) and subsequently joined the project for the final two studies during which the two groups merged. A dominance hierarchy struggle was present within the Edinburgh group, prior to the arrival of the Beekse Bergen group, where displays and fights sometimes resulting in wounding disrupted the research sessions. After the arrival of the Beekse Bergen group, the struggle continued, with the frequency of wounding increasing when the two groups were fully integrated (see Figure 2.3).

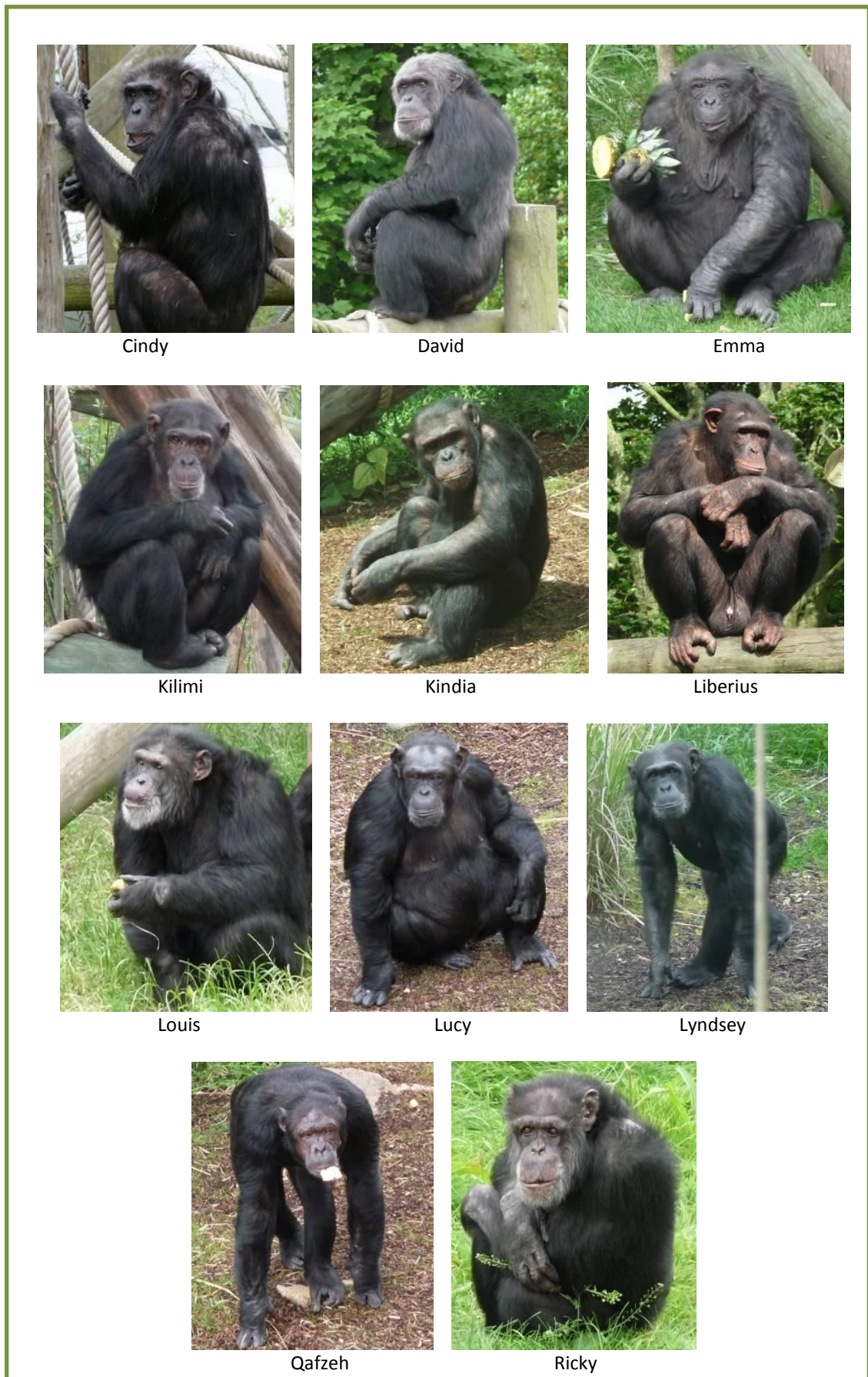


Figure 2.1. Photographs of chimpanzees from the Edinburgh group (in alphabetical order).



Figure 2.2. Photographs of chimpanzees from the Beekse Bergen group (in alphabetical order).

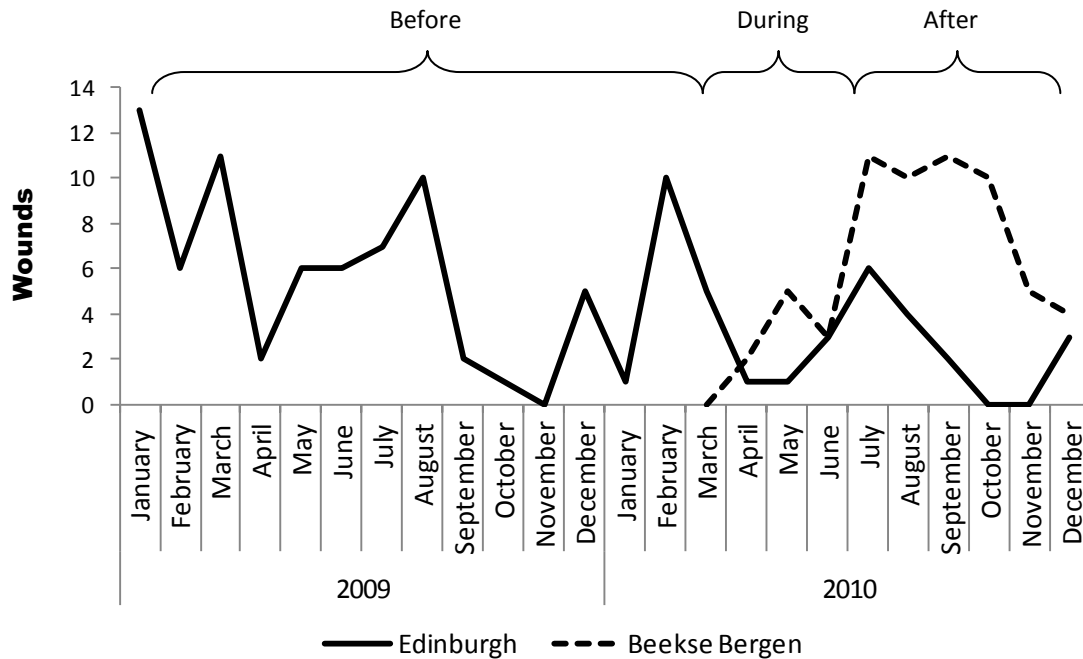


Figure 2.3. Measure of group dynamics as shown by the frequency of wounds recorded per month on chimpanzees from 2009 – 2010 (based on information from the keepers' daily records), labeled as before, during, and after the introductions. For both groups, $n = 11$; with the exception of December where the Beekse Bergen group decreased to $n = 10$ after the death of Bram on 2 December 2010. Individuals wounded multiple times received a data point for each day they were wounded in a given month.

2.3 HOUSING AND HUSBANDRY

Observations of the chimpanzees took place both on- and off-exhibit. This allowed for comparisons of behaviours seen during cognitive training and testing, husbandry training, and when the chimpanzees were not participating in any training activities. Details on the housing and husbandry routines of Budongo Trail are provided below.

2.3.1 HOUSING

The chimpanzees were housed in Budongo Trail, a purpose-built exhibit dedicated to chimpanzee husbandry and research, at RZSS's Edinburgh Zoo. Capable of housing up to 40 chimpanzees, Budongo Trail consists of three indoor enclosures called Pods, an outdoor enclosure, an off-exhibit area with overhead tunnels connecting the Pods, and on-exhibit Research Pods (see Table 2.3 and Figures 2.4 through 2.10). The three interconnected, indoor pods each differ in substrates, climbing frames, lighting, and access routes through off-exhibit or public viewing tunnels. The large outdoor enclosure

includes large, complicated climbing frames, a stream, plant life, and resting platforms at varying heights. The off-exhibit area, consisting of five interconnected areas separated by steel mesh, known as the “bed area”, and overhead tunnels, provide privacy from the public and a quiet area for the chimpanzees to interact with the keepers and other zoo staff (e.g. including positive reinforcement training in the off-exhibit bed areas shown in Figure 2.10). The Research Pods (see Section 2.3.2), where most of the video studies were conducted, are located on the ground floor and can be separated into three separate rooms, if needed (see Figure 2.4, Diagram C).

Natural light fills much of the building, but artificial lighting is readily available and used as a supplement. Artificial lighting was kept on a 12-hour light/dark cycle in all enclosures with the exception of evening functions which were occasionally held in the public areas of Budongo Trail (where lights in the enclosures were sometimes kept on for a few additional hours).

2.3.2 RESEARCH PODS IN BUDONGO TRAIL

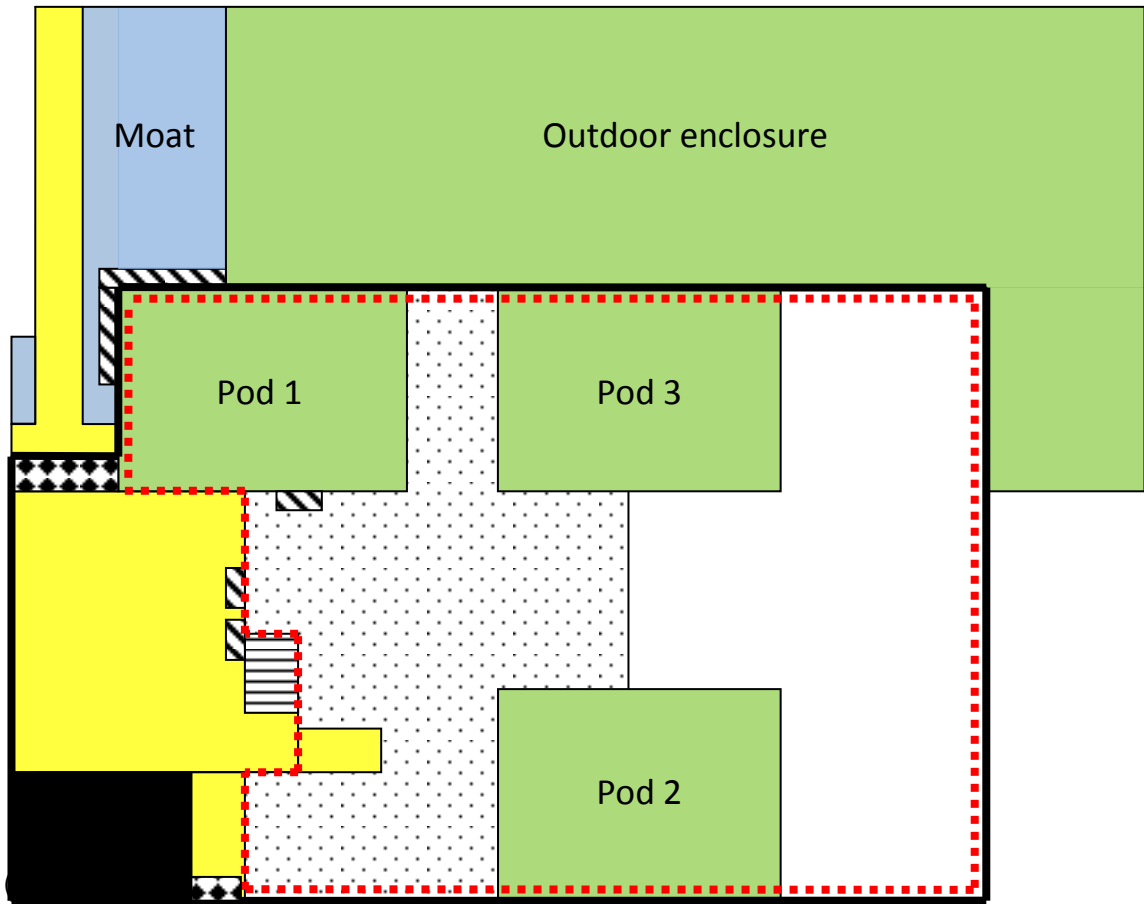
Budongo Trail includes a dedicated research area, called the Research Pods, on full public display, providing visitors with an up-close viewing experience. The Research Pods have four test windows on two walls (see Figure 2.4, Diagram C), each with a food chute to the side and an auditory vent underneath to allow sound to pass through (and also provided another location to deliver food rewards when more than one chimpanzee was at the test window). Visual access to the keepers was provided through test windows where the keepers, when in position in front of window, were in full view. Since the walls of the Research Pods were solid concrete, if the test window was blocked by a test apparatus, visual access was limited to the viewing window directly above the test window (see Figure 2.11) which severely limited observations when chimpanzees were located directly below the test window. Cameras placed in chimpanzee-proof boxes within the Research Pods solved this problem by allowing live feeds of the activities at the test window to stream to a computer screen in the researcher room.

To gain access to the Research Pods, the chimpanzees entered and exited through two rear slides accessible via a built-in ladder. Four test windows, with Perspex measuring 48.9cm by 90.2cm, were located on the walls between the Research Pods and the researcher rooms. Two large windows, each measuring 1.5m x 2.3m, enable visitors to view the research from the public area. Much like the on-

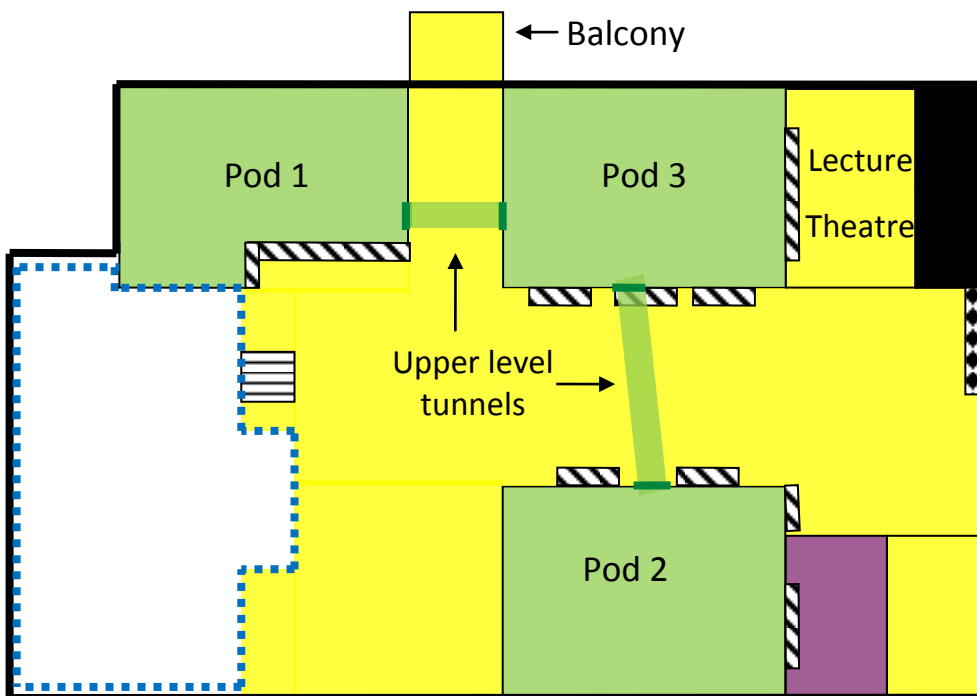
exhibit pods, the chimpanzees are able to watch the visitors, just as the visitors are able to watch the chimpanzees; visitors outside the Research Pods cannot be heard from inside the Research Pods unless contact was made with the viewing window (e.g. visitor bangs on the glass).

Table 2.3. Enclosure details.

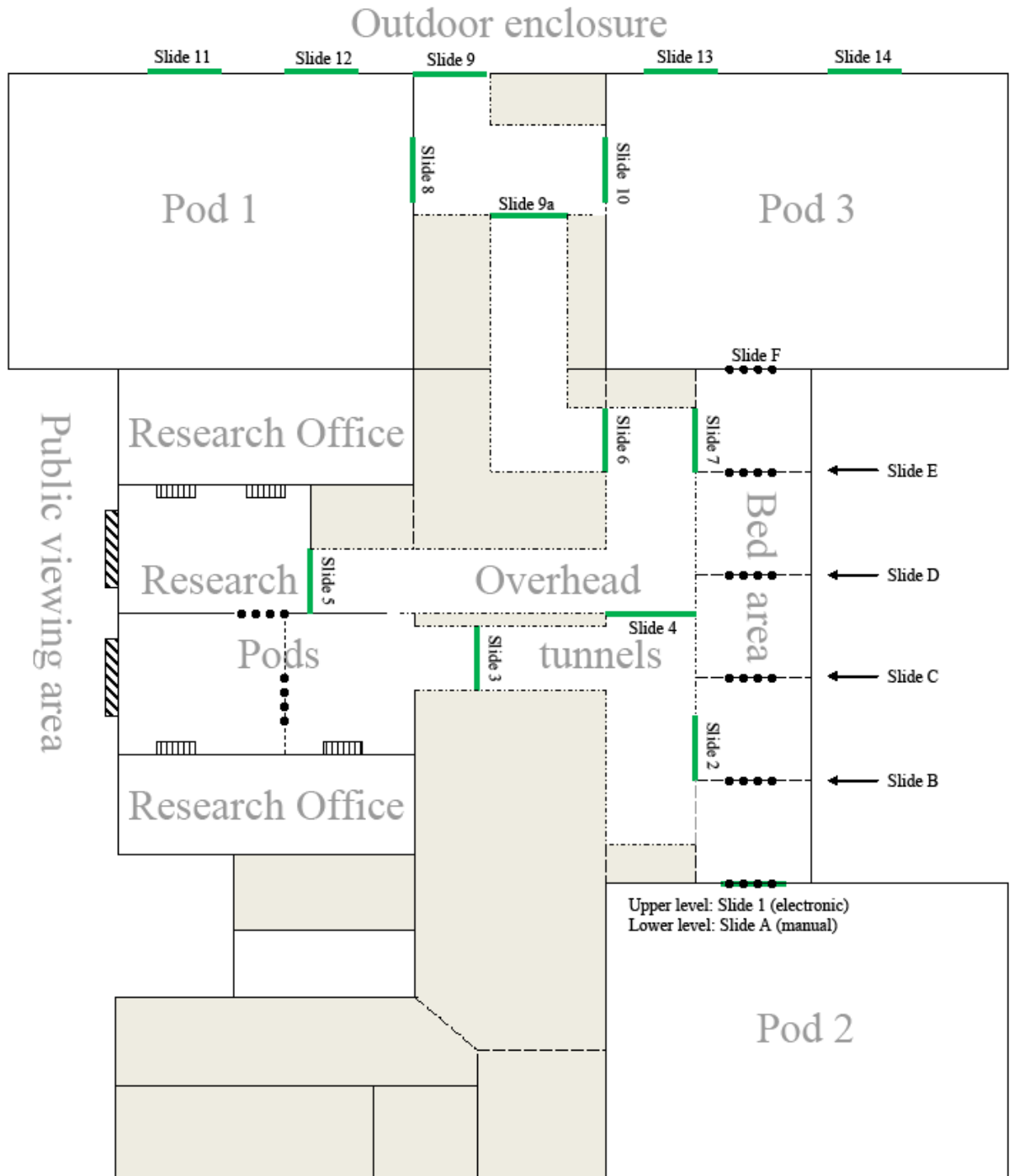
	Pod 1	Pod 2	Pod 3	Outside	Research Pods	Off-exhibit area
Size	120 m ²	120 m ²	120 m ²	1,832 m ²	26.5 m ²	21.45 m ²
Substrate	Compost	Coir	Bark	Dirt, grass, stones	Concrete, straw	Concrete, straw
Plantings	Yes	No	No	Yes	No	No
Lighting (natural)	High	Low	Medium	High	High	Low
Stepped flooring	No	Yes	Yes	No	No	No
Rock wall (usable space)	No	Yes	Yes	No	No	No
Outdoor access (direct)	Yes	No	Yes	--	No	No
Exit/entry points	4	3	5	4	2	4
Hot wires	Yes	No	No	Yes	No	No



(A) Diagram of Budongo Trail's ground floor (dotted red outline highlights the first floor, shown in Diagram B; dotted area highlights the Research Pod and off-exhibit area, shown in Diagram C).



(B) Diagram of Budongo Trail's first floor (dotted blue outline highlights the ground floor, shown in Diagram A).



(C) Diagram of Budongo Trail's research pod and off-exhibit area.

Figure 2.4. Layout of Budongo Trail, not to scale.

- Legend:
- Research Pod/off-exhibit area;
 - Enclosure;
 - Board Room;
 - Visitor Area;
 - Moat;
 - Office/Works Area;
 - Keeper Area;
 - Stairs;
 - Viewing windows;
 - Test windows;
 - Entry/Exit doors;
 - Outline of building;
 - Outline of first floor;
 - Outline of ground floor;
 - Electronic slides;
 - Manual slides;
 - Solid steel/concrete walls;
 - Steel mesh walls;
 - Steel mesh walls (overhead tunnels)



Figure 2.5. Pod 1 (viewed from the Research Office).



Figure 2.6. Pod 2 (viewed from the Board Room).



Figure 2.7. Pod 3 (viewed from the Keeper Area).



Figure 2.8. Outdoor enclosure (viewed from in front of Moat).



Figure 2.9. Outdoor enclosure (viewed from far side of outdoor enclosure, opposite Moat).



Figure 2.10. Research Pods (viewed from the Visitor Area).



Figure 2.11. Perspex of Research Pod test window being unscrewed to allow for the Perspex to be changed (viewed from the Research Office).



Figure 2.12. Off-exhibit bed area during morning husbandry training, “station” and “stay”.

2.3.3 HUSBANDRY

2.3.3.1 TRAINING

The RZSS keepers use positive reinforcement training (PRT), a management technique reliant on the use of rewards when an animal performs a desired behaviour (e.g. McKinley et al., 2003), when working with their animals. PRT is a method of training that provides control and learning opportunities (Bassett & Buchanan-Smith, 2007) and improves animals' abilities to cope with challenges (Laule & Bloomsmith, 2003; Savastano et al., 2003). All training is voluntary; the animals have the choice to end sessions by leaving the area or approaching a closed door to signal a desire to exit.

The Edinburgh chimpanzees were completely naïve to cognitive research and fairly new to all training, having only started to participate in general husbandry training, such as "station" and "stay" (see Figure 2.12), six months prior to the start of the project (C. Gresswell, personal communication, 2008). The keepers hold daily training sessions each morning to work towards getting the chimpanzees to be voluntarily closed into the off-exhibit bed area. This is beneficial for animal management purposes, particularly for veterinary needs. For example, the keepers regularly hold additional afternoon training sessions to work on specific husbandry behaviours (presenting different body parts to be touched by the keeper which can develop into more advanced behaviours, e.g. sonogram of stomach or hand injecting medication). Individuals progressed at their own pace and in relation to individual veterinary needs, for example: Emma was trained to have a nebuliser tube placed into a stoma in her air sac to treat bacterial airsacculitis (Gresswell & Goodman, 2011).

Much like the husbandry training, the keepers worked to train the chimpanzees to be voluntarily closed into the Research Pods. Although it is desirable to carry out cognitive training and testing with one individual at a time (Drea & Wallen, 1999), successful research has been conducted with more than one individual present (e.g. Leighty et al., 2011). Within the duration of this project, the chimpanzees were not successfully trained to be voluntarily closed into the Research Pods, either alone or in subgroups. Subsequently, research training and testing proceeded on a group level with free access to leave.

Research Pod training and testing sessions were announced by two quick whistle blows. The whistle could be heard throughout all enclosure areas, to which the chimpanzees would come down to the

Research Pods if they were inclined to participate. Sessions ranged from 5 – 90 minutes each depending on the group's interest in the research activities. During training, between one to four keepers were stationed at the floor-level, see-through test windows, ready to reward the chimpanzees for a variety of activities. These activities ranged from entering the Research Pods and sitting calmly when the area was still new to the chimpanzees, to correctly targeting to a ball held on the keeper's side of the test window. Targeting to a ball, a similar concept to the keepers' husbandry training methods, was an activity in which the chimpanzees excelled, and was subsequently used as a launching point to teach the chimpanzees how to use a touch screen monitor (described in Chapter 3).

Each chimpanzee was able to end any training or testing sessions and leave the Research Pods at their discretion by moving towards the exit, if the slide is closed, the keepers would open it. The researcher/keeping staff ended the session if the chimpanzee exhibited any harmful behaviour to himself/herself or to the equipment. To end the session, the researcher/keeper staff will turn off all equipment, close the Perspex slide removing chimpanzee access to the monitor, and open the door to the research pod.

2.3.3.2 ACCESS TO GROUP MEMBERS AND ENCLOSURE SPACE

The two groups had access to each other and as much of the enclosure as possible, determined by animal management needs. Pods were closed off for cleaning, maintenance, or delivery of food to the chimpanzees and opened again as soon as the keepers deemed it safe to do so. The chimpanzees were occasionally separated for medical or introduction purposes (these separation periods were kept as short as possible), or if one or more of the chimpanzees opted to stay in the off-exhibit area during morning cleaning when the majority of the group went outside. Outside of zoo opening hours (prior to the merger of the Edinburgh and the Beekse Bergen groups), the chimpanzees were voluntarily closed indoors each night and given the option to sleep in any of the available indoor areas. Once the two groups merged, overnight access to the outdoor area was also provided.

Research sessions were always held as open-access sessions for the entire group to come and go as they pleased. The only exception was for Cindy, during brief morning sessions (approximately 15 minutes long) when she opted to stay in the off-exhibit area while the rest of the group was outside. During this

time Cindy voluntarily entered the Research Pods and remained there while the door was closed for the duration of the session. This was beneficial as it provided an opportunity to try out methods with a particularly well-motivated and attentive participant (Cindy) before presenting activities in a group context. The Research Pods were only available during research sessions, however during the introduction process, the Research Pods were no longer used for cognitive and training purposes and instead were used as additional enclosure space to help move the groups around the enclosure as needed.

2.3.3.3 ENVIRONMENTAL ENRICHMENT AND BEDDING MATERIALS

Environmental enrichment is a method used to increase choice and control to draw out species-typical abilities and enhance welfare (BHAG, 1999). From a variety of puzzle feeders to herb-filled parcels, and climbing structures, enrichment played a significant role in the lives of the Budongo Trail chimpanzees in the everyday activities provided by keepers. In addition to the substrates in each pod, bedding materials were provided daily. Bedding materials are enrichment items that encourage the chimpanzees to participate in species-typical nesting behaviours. The materials provided varied and included straw, eucalyptus branches, hay, clothing, and wood wool. Outside of specific protocols during studies of nesting preferences and behaviour studies (Lock, 2010; S. Gregory, personal communication, 2009), any bedding that was not used or remained clean and usable stayed within the enclosure as an option for bedding the next night.

Enrichment was also a part of each research session. While training and cognitive testing do not automatically produce images of species-typical behaviours that the previous examples may evoke, they are forms of enrichment that challenge the mind and encourage the animals to think; an activity that certainly is species-typical (Poole, 1998; Ross et al., 2010; Yamanashi & Hayashi, 2011). By incorporating cognitive challenges into a variety of activities we can facilitate learning and explore our animals' cognitive abilities.

2.3.3.4 CLEANING

Subject to management needs and the ability to safely move chimpanzees from one area to another, enclosure areas were spot cleaned on a daily basis (removal of faeces, discarded food, used bedding

materials, etc.) with a deep clean occurring once a week. Safe4 was used to disinfect floors, walls, and furnishings. Natural substrates within the pods were turned daily. After cleaning, the Research Pods and off-exhibit bed areas were covered with a layer of wood shavings, straw, or wood wool to facilitate foraging and provide an absorbent material for urination and defecation.

2.3.3.5 DIET

In order to remain consistent during the transition period of the Beekse Bergen group, the precise diet composition for each group differed and was slowly adjusted to the same diet as the groups merged. Their feeding schedule over the course of a week included fruits, vegetables, primate pellets (Trio Munch), and protein (see Appendices D1 and D2). An average of five kilograms of food per chimpanzee were offered across five to eight feeds per day at various times and locations. Total weight was distributed across each group as determined by the number of chimpanzees in each group. Access to water was available *ad libitum* through drinkers placed throughout the enclosure and diluted juice or tea was made available during various times of the day, including being used as a reward during husbandry training. Food rewards offered during training and research sessions varied according to the type of session (see Appendix D3). The primary food rewards used during research sessions (dried figs) were primarily used for training purposes and only offered on rare occasions within their daily diet.

2.4 STUDY METHODOLOGY

Due to the variety of topics covered in this thesis, a diverse range of research methods were used across studies and each is therefore described in more detail in the relevant chapter. However, a general description of the central observational protocol, data collection, and sampling methods is supplied in this chapter.

2.4.1 OBSERVATIONAL PROTOCOL

Prior to any data collection, the chimpanzees were habituated to the researcher's presence. It was deemed appropriate for the researcher to remain visible to the chimpanzees during all phases of the project given that the Research Pods were on public display and that one of the animal management goals was to help the chimpanzees to be comfortable in any situation (e.g. multiple people present

during training). Data collection took place in various locations throughout Budongo Trail allowing the researcher to observe the chimpanzees from several different vantage points (see Table 2.4). Specific details for each study are provided in subsequent chapters.

2.4.2 DATA COLLECTION

2.4.2.1 BEHAVIOURAL DATA

Data collection took place at different times for each study, but remained within the working hours of the zoo: April – September, 08:00 – 18:00 hours; March and October 08:30 – 17:00 hours; November – February 08:30 – 16:30 hours). Behavioural data were collected using either Noldus Observer XT8 software or paper check sheets (see Appendix B) in four different areas of Budongo Trail: the Research Pods, the chimpanzee enclosures (Pods 1, 2, 3, and outside), the public viewing areas, and the off-exhibit areas (see Table 2.4). Noldus Observer XT8 software was selected for its ability to record state and event behaviours and retrospectively analyse sessions recorded on video. Paper check sheets were used when there were multiple observers and when the software programme was not able to collect all of the data needed, particularly when behavioural modifiers were non-mutually exclusive, such as noting which chimpanzees were present during a scan (Martin & Bateson, 2007). Questionnaire and observational methods to assess visitor numbers were used during the Public engagement with science study (described in Chapter 5). In relation to the specific research questions, the behaviours recorded varied across the studies (see Table 2.5).

2.4.2.2 DOMINANCE RANKINGS

Individual dominance ranks (see Appendix A) were gauged by the primary researcher (Herrelko) and three keepers from Edinburgh Zoo in 2009 based upon extensive observations of chimpanzee interactions. For the Beekse Bergen group, dominance ranks were calculated based on dominance ratings from chimpanzee personality surveys completed by two keepers in 2010 (see Chapter 6). Each set of ranks represent the status of each chimpanzee before the two groups met (Edinburgh in 2009 and Beekse Bergen in 2010). The rankings were split into categories of high, medium, and low (see Table 2.2).

The Edinburgh keepers were requested to rank the chimpanzees (only those they worked with full-time for at least six months) based on their observations of each individual's interactions within the group. For example, if an individual instigated displays or fights and was able to displace others in order to gain ideal sleeping spots or feeding locations, that individual was likely to be higher ranking than the one being picked on or displaced. The scores for each group member were averaged and provided an overall rank from all raters (see Appendix A1).

The Beekse Bergen keepers completed a personality survey (based on Weiss et al., 2009) where they were asked to rate each chimpanzee on a number of behaviours, including dominance (see Chapter 6). In the survey, dominance was defined as, "Subject is able to displace, threaten, or take food from other chimpanzees. Or subject may express high status by decisively intervening in social interactions." With a rating scale from 1 (absence of trait) to 7 (large amounts of trait), rankings were calculated by averaging the two scores for each chimpanzee and listing the highest rank for the highest average score through the lowest rank for the lowest score (see Appendix A2). When an average score was the same for two individuals (a male and a female), the higher rank went to the male.

Table 2.4. Study locations.

	Study location				Researcher location
	Research Pods	Pods 1, 2, 3, and outside	Visitor areas	Off-exhibit areas	
CH 3: Cognitive activities with research naïve chimpanzees	Yes	No	No	No	Research office
CH 4: Welfare assessment during the development of a cognitive research programme	Yes	Yes	No	Yes	Visitor areas; Research office; Off-exhibit area
CH 5: Assessing public engagement with science	No	No	Yes	No	Visitor areas
CH 6: Behavioural predictors of introduction outcomes	No	No	No	Yes	Off-exhibit area
CH 7: Welfare implications of chimpanzee introductions	No	Yes	No	Yes	Visitor areas; Off-exhibit area

Table 2.5. Definitions and recording categories for the behaviour terms used in each study.

Type	Term	Definition	Recording Category	Chapter
Groom	Allogroom	Picking through hair or at skin of another individual and removing debris with hands and/or mouth. Does not include pulling hair (Ross & Lukas, 2001).	State	7
Personality factors	Dominance	Positive loading: Bullying, decisive, dominant, independent, intelligent, manipulative, persistent, stingy	Survey	6
		Negative loading: Anxious, cautious, dependent, fearful, submissive, timid, vulnerable		
	Extraversion	Positive loading: Active, affectionate, friendly*, imitative, playful, sociable	Survey	6
		Negative loading: Depressed, individualistic*, lazy*, solitary		
	Conscientiousness	Positive loading: Predictable*	Survey	6
		Negative loading: Aggressive, clumsy*, defiant, disorganised, distractible, erratic, impulsive*, irritable*, jealous, quitting		
	Agreeableness	Positive loading: Conventional, gentle, helpful*, protective, sensitive*, sympathetic	Survey	6
	Neuroticism	Positive loading: Autistic, excitable	Survey	6
Negative loading: Cool, stable, unemotional				
Openness	Positive loading: Curious, innovative, inquisitive, inventive	Survey	6	
Proximity to others	Alone [^]	Only the focal animal is visible on the video recording of the session, no other chimpanzees are visible.	Event	3
	Near others [^]	At least one other chimpanzee is visible with the focal animal.	Event	3
R/R	Regurgitate	Voluntary retrograde movement of food and/or fluid from the esophagus or stomach into the mouth, the hands, or a substrate (Lukas, 1999).	Event	7
	Reingest	Eat regurgitated matter (Lukas, 1999; Hill, 2007).	Event	7

Research	Interest in research	Presence in the Research Pods during a research session (including active participants and those who observed). For location-specific categories, see Table 4.4).	State	4
Self-directed behaviours	Scratch	Rake one's own hair or skin with fingernails including mainly movements of the hands and fingers, sometimes including arm movements (adapted from Baker & Aureli, 1997).	Event	4 & 7
	Rub	A self-touch, usually to the face, that does not involve tips of digits (adapted from Hopkins et al., 2006).	Event	4 & 7
	Self Groom	Picking through own hair or at skin and removing debris with hands and/or mouth. Does not include pulling hair (adapted from Ross & Lukas, 2001).	State	4 & 7
	Yawn	Open mouth and expose teeth in a gaping movement, while inhaling air. This is followed by an immediate exhalation of air (adapted from Baker & Aureli, 1997).	Event	4 & 7
Social behaviours	Aggressive	Display behaviours including sway and pant hoot, chase, hit, bite, charge (chimps or objects), stomp foot, fight, kick, or jump over (Brent et al., 1997).	State	6
	Affiliative	Approach, follow and smell with touching, embrace, hug, groom, mouth, pat, play, play invite, copulate, erection display, inspect genitals, mount, and kiss (Brent et al., 1997).	State	6
	Neutral*	No social behaviours exhibited.	State	6
	Not Present*	Not physically in the introduction area.	State	6
Touchscreen behaviours	First touch	The initial contact the chimpanzee makes with the test window (Perspex or touchscreen itself) when prompted by the main screen (i.e. quadrants with four red circles in the centre of each one).	Event	3
	Correct touch	A touch that activates a video (must touch the red circle). Note: The ChimpPlayer software will not play a video unless a correct touch occurs.	Event	3
	Incorrect touch	Any touch to the touchscreen or Perspex in the test window that does not activate a video.	Event	3
	Touch while video is playing	Any touch to the touchscreen or Perspex in the test window when the video is playing full screen, except when a hand is just resting on the ledge of a hole in the Perspex.	Event	3
Vigilance	Vigilance	Orient face towards the door of the Research Pods. Face must be turned in such a way that at least half of the face is in view of the camera (approximately a 90 degree angle between the camera and the Research Pod door).	Event	4
Watch	Watch	Face oriented towards the monitor.	State	6

Note: An asterisk (*) indicates an item omitted due to low inter-observer reliability; a caret (^) indicates an item recorded as part of the touchscreen behaviour terms to identify differences in performance as a result of the social context; R/R was only used after the arrival of the Beekse Bergen group, who exhibited these behaviours while the Edinburgh group did not.

2.4.3 SAMPLING METHODS

Sampling and recording rules differed across studies (see Table 2.6): The cognitive activities (Chapter 3) incorporated focal sampling of each chimpanzee with continuous recording of all occurrences of mirror-directed behaviour, behaviour sampling with continuous recording of correct and incorrect touches to the screen, and scan sampling with instantaneous time sampling to record chimpanzee interest in the cognitive tasks. The study assessing welfare during the development of a cognitive research training programme (Chapter 4) incorporated focal sampling of each chimpanzee with continuous recording to capture all-occurrences of self-directed behaviours. In addition to online questionnaire data collection, the study assessing public engagement with science (Chapter 5) also incorporated behaviour sampling with continuous recording of visitors entering Budongo Trail, noting details of age, gender, and group composition.

The study of behavioural predictors of introduction outcomes (Chapter 6) incorporated behaviour sampling with continuous recording of aggressive, affiliative, submissive, and self-directed behaviours, and scan sampling with instantaneous time sampling to record chimpanzee levels of interest in the video provided. The study examining welfare implications of chimpanzee introductions (Chapter 7) incorporated focal sampling of each chimpanzee with continuous recording of self-directed behaviour and scan sampling with instantaneous time sampling to record their activity.

Focal animals were selected based on visibility and whether or not they were already observed during that session or within a particular time period (to ensure observations were balanced across the course of the day). If, after data collection began, the focal animal left the area and was not in view, the researcher would move on to a second focal animal. This occurred immediately during Research Pod sessions, as total session time was limited. If the first focal animal returned to the research pod within 30 seconds of their departure, data collection would resume for that animal and any data collected for the second animal would be omitted. During non-Research Pod sessions the researcher would only move on to another focal animal if the focal animal had not been in view for three minutes. After three minutes, the researcher would start observations with another focal animal and attempt to observe the original focal animal after the second focal animal observation was complete.

All instantaneous time sampling durations were consistent at 30 seconds across all studies using scan sampling. Scan sampling was used to capture state behaviours that were longer in duration (i.e. resting, location, etc.) as opposed to all occurrences or behaviour sampling for brief duration events (e.g. scratching; Martin & Bateson, 2007; see Table 2.5). This produced an estimated percentage of time the group (or each individual) spent within a specific location or engaged in a particular behaviour when visible to the researcher. Behavioural events were recorded as independent actions or in bouts, where a break in the observed behaviour must occur before a new bout could begin (e.g. a scratch on the left arm that is immediately followed by a scratch of the left leg was counted as one single event where as a scratch on the left arm followed by a face rub and another scratch was counted as three events: scratch, rub, scratch). Recording all occurrences of event behaviours produced a frequency at which the behaviour occurred during the observation session, taking time in view into account and allowing a rate per hour to be calculated.

Table 2.6. Sampling, recording rules, and behaviour captured within each study.

	Sampling rule	Recording rule	Behaviour captured
CH 3: Cognitive activities with research naïve chimpanzees	Focal	Continuous	Monitor-directed behaviour (all-occurrences)
	Behaviour	Continuous	Correct/incorrect screen touches
CH 4: Welfare assessment during the development of a cognitive research programme	Focal	Continuous	SDBs (all-occurrences)
	Scan	Instantaneous (scans every 30s)	Chimpanzee interest
CH 5: Assessing public engagement with science	Behaviour	Continuous	Visitors entering Budongo Trail (age, gender, and group composition)
CH 6: Behavioural predictors of introduction outcomes	Behaviour	Continuous	Aggressive, affiliative, submissive, and self-directed behaviours
	Scan	Instantaneous (scans every 30s)	Chimpanzee interest in videos
CH 7: Welfare implications of chimpanzee introductions	Focal	Continuous	SDBs (all-occurrences)
	Scan	Instantaneous (scans every 30s)	Activity

2.4.4 DATA ANALYSIS

2.4.4.1 STATISTICAL ASSUMPTIONS

All data were assessed with the Kolmogorov-Smirnov test for normality and Levene's test for homogeneity of variance. When necessary, data were transformed ($\log+1$) in order to perform parametric statistics whenever possible. Transformations are noted along with the analyses, however, regardless of transformation status, graphs represent untransformed data. When data assumptions could not be met, nonparametric statistics were used with means being reported alongside medians when appropriate (Field, 2009).

2.4.4.2 INTER-OBSERVER RELIABILITY

Inter- and intra-observer reliability (IOR) was tested to ensure that the behaviours analysed were being reliably measured across and between observers. To do this, the observed behaviours were given precise definitions (see Table 2.5). When IOR data were available to test between two individuals or two duplicate sessions for a single observer, a Pearson correlation was calculated. When IOR data were available to test across more than two individuals, Intraclass Correlations were calculated (Shrout & Fleiss, 1979). Behaviours that did not reach a high level of agreement between observers (a Pearson correlation of less than 0.7; Martin & Bateson, 2007) were not analysed. Details are provided in individual chapters.

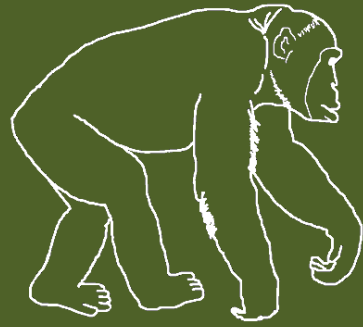
Inter-observer reliability was also calculated for dominance rankings across four raters for the Edinburgh group and two raters for the Beekse Bergen group. Each keeper's ratings for the Edinburgh group were compared to the researcher's ratings with a high level of reliability: keeper 1, CG ($r = 0.96$, $n = 11$), keeper 2, SR ($r = 0.87$, $n = 11$), keeper 3, SG ($r = 0.99$, $n = 11$). The Beekse Bergen group ratings were compared keeper 1, WB to keeper 2, JKH producing an acceptable level of reliability ($r = 0.74$, $n = 11$). Since the two sets of ranks were collected in a different manner (Edinburgh ranking 1-11 and Beekse Bergen completing personality survey including a rating for dominance), the personality surveys completed for the Edinburgh group (see Chapter 6) were used to compare the average score for dominance to the overall rankings. The comparison produced an acceptable level of reliability between

the two methods ($r = 0.87$, $n = 11$), suggesting that using the dominance trait score from the personality survey is equivalent to having rankings supplied directly.

2.4.5 ETHICAL CONSIDERATIONS

Ethical considerations were taken into account throughout the duration of the project as animals may exhibit stress-related behaviours in response to task difficulty during cognitive activities (Itakura, 1997; Leavens et al., 2001; Yamanashi & Matsuzawa, 2010) and the introduction of unfamiliar chimpanzees to each other can be a stressful and challenging process (Brent et al., 1997; Seres, 2001). Each study was deemed appropriate given that chimpanzee participation was voluntary and worked within the existing parameters of zoo management. Additionally, all management decisions for the introduction process were determined by the keepers and the researcher or keeping staff could end the research sessions at any time (e.g. if the chimpanzees exhibited any harmful behaviour).

For research with human participants, the researcher explained that participants could withdraw from the study at any time and provided a verbal debriefing after completion of the study (or withdrawal). For the Chapter 5 study participants, a debriefing card (see Appendix F2) was also provided to reiterate the study's objective and provide contact details and the project's website in the event that they wanted more information. All studies were approved by the University of Stirling's Psychology Ethics Committee and RZSS's Department of Animals, Education, and Conservation, and abided by ASAB (ASAB, 2006) and BPS ethical guidelines (BPS, 2010).



CHAPTER 3

COGNITIVE RESEARCH WITH NAÏVE CHIMPANZEES



COGNITIVE RESEARCH WITH NAÏVE CHIMPANZEES

3.1 ABSTRACT

Cognitive research with chimpanzees has been studied in both group and individual settings. While most of these studies involve individuals who are experienced with research from an early age, the literature exploring the development of cognitive programme with research-naïve chimpanzees is sparse. This study aimed to train research-naïve chimpanzees to use a touchscreen monitor, in a group setting, to make choices and select live-video feeds to watch. After over one year of research training activities with three months dedicated to touchscreen activities, the group did not use the touchscreen to make choices between stimuli. The type of video feed did not impact selection, but the location of the video (i.e. which quadrant) did matter, where the right side (closest to the food reward) was selected the most. In terms of group testing, the presence of others impacted upon access to the monitor but not accuracy of performance. A group testing environment is encouraged to benefit from early training stages with research- and training-naïve chimpanzees.

3.2 INTRODUCTION

3.2.1 COGNITIVE RESEARCH WITH CHIMPANZEES

Comparative psychology compares cognitive capacities across species (Watson, 1913). As researchers, we are interested in nonhuman primates, particularly chimpanzees, because of their many similarities to humans, but we are also motivated to explore the ways in which we might be unique (Gibbons, 1998). Studying behaviour provides us with a unique glimpse into the animal mind and allows us to explore their cognitive abilities, which in turn, helps us to understand ourselves. Cognitive studies with nonhuman primates have come in many different shapes and forms including topics like attention (Kelleher, 1958), communication (Gardner & Gardner, 1969; Fouts, 1997), cooperation (Melis et al., 2006), deception (Woodruff & Premack, 1979), memory (Menzel, 1973; Kawai & Matsuzawa, 2000; Inoue & Matsuzawa, 2007), numerical competence (Boysen & Berntson, 1989), problem solving (Kohler, 1925), social learning (Whiten et al., 1999), and tool use (Boesch & Boesch, 1990). For a detailed review of physical and social cognition, see Tomasello and Call (1997).

As technology advanced, so did methodological techniques, for example, by incorporating computers with touchscreen monitors and videos into many research projects. Computers are not just a tool that allows paradigms to be tested (e.g. lexigrams on monitor serving the same function as symbols on board); they also allow new paradigms to be explored (e.g. eye tracking studies: Kano & Tomonaga, 2009). Touchscreens in particular, provide opportunities for researchers to ask new questions and mentally stimulate animals in different ways (e.g. Iversen & Matsuzawa, 1996; Sousa et al., 2003; Inoue & Matsuzawa, 2007, Parr et al., 2010). Videos have been used as enrichment and in cognitive research where they have been shown to: occupy the attention of captive chimpanzees (Bloomsmith et al., 1990; Bloomsmith & Lambeth, 2000), play a role or accelerate learning through social observation (Price et al., 2009; Perlman et al., 2010), explore self recognition (Eddy et al., 1996), and provide information through a representational understanding of images (Menzel et al., 1978; Menzel et al., 1985; Cook & Mineka, 1989; Nagell et al., 1993; Kuhlmeier et al., 1999; Morimura & Matsuzawa, 2001; Poss & Rochat, 2003; Price & Caldwell, 2007). However, since computer monitors and televisions are designed with humans in mind, researchers should be aware of how their study animals perceive the stimulus. As chimpanzees have the same colour vision receptor peaks and flicker-fusion thresholds as humans (D'Earth, 1998), they should perceive objects on the screen just as humans do.

Research with chimpanzees has included videos of conspecifics to study cognition for the past few decades, but only recently has the presentation of live images been incorporated (Hirata, 2007). Hirata (2007) used television monitors in addition to mirrors in a self-recognition task. With the chimpanzee participants successfully exhibiting self-exploratory behaviours, when viewing close-up and distant images of themselves on a live-video feed, just as they had with mirrors, it is suggested that self-recognition is not a function of the test apparatus. The horizontally flipped image of a video monitor, showing a smaller than life-size chimpanzee as others see him/her (rather than the reflection in a mirror), different viewing angles, and the addition of objects (plastic tubes and toys provided for the chimpanzees to pick up and manipulate as an extended means of contingent body movement) did not reveal any significant differences in chimpanzee reaction compared to traditional mirror self-recognition tests. These findings suggest that understanding different perspectives play a role in being able to comprehend both reflections and televised images.

Physiological and behavioural responses to video footage suggest that video content can be meaningful and effective: Skin temperature decreases when watching negatively valenced videos (e.g. chimpanzees being injected with needles), signifying negative sympathetic arousal (Parr, 2001). Images of facial expressions can be matched to the emotional meaning within a video (e.g. an object or action with a positive or negative valence; Parr, 2001). Contagious yawning occurs in chimpanzees when they watch footage of other chimpanzees yawning (Anderson et al., 2004; Campbell & de Waal, 2011). These studies were successfully performed with prerecorded footage that provided control over the stimuli not otherwise possible with live observations. However, live-video footage can be a helpful research tool to assess reactions to their environment. Monitoring others is important to animals (Chance, 1967). By providing visual access to areas where the focal chimpanzee is not, we can essentially expand their ability to monitor the fission-fusion activities of other group members and assess their ability to understand the concept of “live” video. Even without relying on an interest in fission-fusion dynamics, live-video feeds have been a useful tool to help chimpanzees find a hidden object within reach that they could view on the television monitor (Menzel et al., 1985).

Although chimpanzees are curious animals (e.g. Morgan & Sanz, 2003), whether or not they are intrinsically interested in an activity could ultimately determine the success or failure of a research project. Determining what is important to them is interesting from an animal management and comparative cognition standpoint. Visual preference testing has a long history (Fantz, 1964; Humphrey, 1972; Balling & Falk, 1982; Fujita, 1993; Tanaka, 2003; Paukner et al., 2005). By measuring interest, we can gain a better picture of what is important to animals and use that information to better their welfare and understand their experiences. When considering photographs, chimpanzees who were hand raised have a visual preference for humans over chimpanzees (Tanaka, 2003), no doubt resulting from the strong influence of their previous social experiences.

3.2.2 GROUP TESTING

One welfare issue that is important to both zoo staff and researchers is whether animals should be separated for training and testing. Previous articles on research in group versus individual settings have revealed that: In a group setting animals tend to be more relaxed than in an individual setting (Prescott

& Buchanan-Smith, 1999; Schapiro et al., 2003), for example, heart rate decreased when animal subjects had visual contact to conspecifics (Scott et al., 2003). While being in a group provides opportunities to learn through observation (Prescott & Buchanan-Smith, 1999; Whiten, 2000; Matsuzawa, 2002; Savastano et al., 2003), individual testing allows social influences on testing to be removed (Drea & Wallen, 1999; Schapiro et al., 2003). However, separation from group members might be stressful for some individuals and may potentially alter study results (as reviewed by Rennie & Buchanan-Smith, 2006a).

Social factors may thus have a positive or a negative influence, for example: for rhesus macaques (*Macaca mulatta*), having group members around can inhibit performance, where submissive animals might “play dumb” when more dominant ones are around during an associative learning task (Drea & Wallen, 1999). For example, for chimpanzees, more SDBs were exhibited in crowded compared to less crowded enclosures (Aureli & de Waal, 1997); and for orangutans (*Pongo pygmaeus*), group testing has previously lead to aggression and competition over limited resources (Tarou et al., 2004). On the other hand, animals may become stressed when separated and this may be detrimental to learning (Prescott et al., 2005). Of course, it can be time consuming to set up individual testing, and individuals may also refuse requests to be separated (Schapiro et al., 2003). Zoo researchers have started to look at methods in which cognitive testing can be conducted without isolating animals (Fagot & Wallen, 1991; Andrews & Rosenblum, 1994; Drea & Wallen, 1999; Drea, 2006; Fagot & Paleressompoulle, 2009). At the time of the project, the majority of our study animals were only prepared to engage in research activities on a group level.

3.2.3 STUDY AIMS

At the onset of the project, Budongo Trail housed a group of research-naïve chimpanzees that were relatively new to training (see Chapter 2). The ultimate aim of the project was to provide this group of chimpanzees with a video camera that they could carry around their enclosure filming anything they liked; it was the hook to encourage people to watch a documentary about chimpanzee cognition and social structure. Within this context, we created studies to explore how this group responded to video images. The study aimed to examine the performance of research naïve chimpanzees using a

touchscreen monitor to make choices in a group research setting. This concept was explored in four analytical categories in which we identified the following questions and hypotheses:

ANALYSIS 1: INTEREST IN RESEARCH

How often were the chimpanzees present during the cognitive testing activities?

ANALYSIS 2: PERFORMANCE

After a period of initial training to help provide familiarity with the research tasks, (a) which chimpanzees reached the 70% criterion level? and (b) Did they wait to touch the screen (e.g. activate another video) until prompted by the main screen of choices.

ANALYSIS 3: VIDEO CHOICES

The chimpanzees would exhibit a preference for different live feeds.

ANALYSIS 4: GROUP TESTING

The presence of others would impact performance in their (a) ability to access and (b) accurately use the touchscreen.

3.3 METHODS

3.3.1 STUDY ANIMALS

The study animals were 11 chimpanzees (*Pan troglodytes*) from the Edinburgh group, 6 males and 5 females ranging in age from 9 to 47 years old (mean = 26.09; SE mean = 3.84) at the onset of the project, May 2008. Additional information on the group, their management, and housing conditions is described in Chapter 2, General Methods.

3.3.2 APPARATUS

Paper checksheets (see Appendix B1) were used to record activity with the touchscreen monitors and group presence. Four Axis 206 IP cameras placed throughout Budongo Trail and connected to the building's local network were used to feed live video to the Research Pods. A Toshiba Satellite Pro U400 computer operated three programmes: (1) a training programme using Microsoft's PowerPoint to learn

how to use a touchscreen (see Section 3.3.3.1), (2) ChimpPlayer, a custom-designed user interface for selection of the video feeds (from Hmelyoff Labs), and (3) Microsoft's Excel to randomise the order of video presentation. Video feeds were viewed on a 19" open-frame flat screen touchscreen monitor (Elo 1939L) that was mounted on a steel L-shaped cart. The test window housed a 12mm sheet of Perspex as the barrier between the chimpanzees and the monitor, with four holes (6.4 cm in diameter) to allow interaction with the monitor. A Sony HD 3CMOS colour video camera was used to video tape Research Pod sessions onto an Apple Xserve computer, which were later reviewed using QuickTime Player 7.6.4 on the Toshiba computer.

3.3.3 RESEARCH DESIGN

3.3.3.1 TRAINING

At the beginning of the study, the chimpanzees were slowly introduced to the Research Pods in an open-access group context where individuals could come and go as they pleased and food rewards and verbal praise were offered upon entry. Training, still in the group context due to practical constraints, gradually built up to include targeting activities (i.e. touching a ball, the target, that a trainer held up against the other side of the Perspex test window) where behaviours could be shaped in preparation to use the touchscreen (e.g. rewarding gentle touches instead of the heavy handedness that chimpanzees sometimes use). Before the live-video feeds were presented, target training without the monitor occurred for 12 months and with the monitor for 2 months.

To transition from targeting to a physical object at the test window to targeting to the monitor, we designed a looping 20 slide PowerPoint presentation with a photo of the target on each slide in differing places (see Figure 3.1). Once the target was touched, it would bring up a different slide, prompting the chimpanzees to repeatedly touch the target, in different locations, for a food reward.



Figure 3.1. Training programme with a picture of a hand holding the red ball target.

Once the chimpanzees became familiar with this activity and were targeting to the red ball on the screen, the targets were replaced with a split screen of four pictures of familiar individuals (Budongo Trail staff and the researcher) with red circles on them to continue the rule that touching the red circle or ball earns a reward (see Figure 3.2) to mimic the format of what the chimpanzees would see when the live feeds were presented. Once selected, the picture was shown full screen for up to 10 second (in increasing increments of 2s, 5s, and 10s) before the main screen of choices (i.e. four pictures with red targets) was presented. Time outs (i.e. turning off the monitor and waiting a few seconds) were used to refocus the training session if needed (e.g. if superstitious touching occurred where the chimpanzees repeatedly responded incorrectly).



Figure 3.2. Training programme with pictures of familiar individuals in all four quadrants.

Prior to target training with the monitor, six 30-minute self-recognition sessions were held to introduce the concept of a live-video feed. Live-video feeds of the chimpanzee in the Research Pods were displayed on the monitor and alternated between a close up of the upper body and a wide angle view from the side. Rewards were provided on a random schedule. Despite repeated interest in the Research Pods during this time (i.e. entering the research area during each session, sometimes several times, with limited interaction with the monitor), no self-directed behaviours were seen in relation to the monitor, as would be expected based on previous research (Hirata, 2007). However, this does not mean the group is unusual because other chimpanzees have been known to not show clear evidence of self recognition (Swartz & Evans, 1991). As a result, this portion of the project was omitted from the chapter as it mainly served as a step towards the video choice study by providing them with experience watching live-video feeds.

3.3.3.2 SESSIONS

Individual training sessions with Cindy (11 total) to pilot the training methods for the group were held up to two times per week lasting 10 – 15 minutes. Group training sessions (19 total sessions with the

monitor) were held up to three times per week lasting 20 – 60 minutes, dependent upon chimpanzee interest and keeper availability. Group video choice sessions (24 total) were held up to four times per week and each lasted 30 minutes; a small percentage of the training time most computer-trained chimpanzees have experienced (e.g. Primate Research Institute: Matsuzawa, 1985; Fujita & Matsuzawa, 1990; Tomanaga & Matsuzawa, 1992; Iversen & Matsuzawa, 2001). While our training and testing time was brief, the use of intuitive choice tasks, with no right or wrong answer in video selections, would likely require less training time than many of the more complex tasks performed by experienced chimpanzees.

3.3.3.3 VIDEO CHOICE ACTIVITY

The touchscreen monitor screen was split into four sections with each quadrant (Q) representing a number (see Figure 3.3) that corresponds to the placement of different video feeds. Twenty-four sessions were held to allow the four live feeds to be presented in every quadrant combination possible where the order was randomly determined using Excel's random number generator and sorting feature.

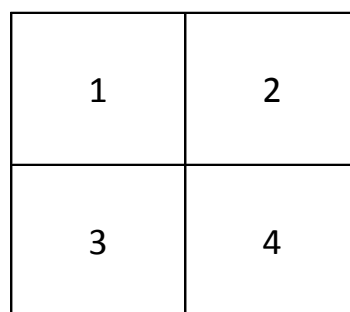


Figure 3.3. Video location quadrants on the touchscreen monitor.

The main screen, much like the training sessions with still pictures, consisted of four screen captures of the live video feed with a red circle on each quadrant. Once a selection was made, the live feed corresponding to that screen capture was shown full screen for 10 seconds before automatically reverting back to the main screen of choices, which remained in place until a new selection was made. If a touch was made to the monitor while a video was playing, nothing would happen. Selections to activate a video could only be made when prompted by the main screen. The chimpanzees were presented with a free-choice task (e.g. Tanaka, 2003) where they were presented with four still images

representing four live-video feeds. Touching any of the four images (when prompted by the main screen with red targets, see Figure 3.4) resulted in a food reward regardless of which image and corresponding video was selected.

With the exception of the food preparation feed, the cameras for the live-video feeds were strategically placed to capture an angle that the chimpanzees would have seen before as a part of their everyday movement around the enclosure. The four feeds consisted of: (1) The outside enclosure; (2) an inside enclosure, Pod 1; (3) the food preparation area, a part of the enclosure that they have never seen before; and (4) a black screen (see Figure 3.4). Camera locations remained the same for all sessions.

Group testing was held for the majority of the research sessions (43 out of 54). At least two trainers were on hand to avoid congestion at the primary test window where the touchscreen was housed.

During video choice training and testing, the chimpanzees had the option to participate in similar activities at multiple test windows: Basic targeting activities were held at the secondary test windows where the same food rewards and verbal praise could be earned as at the primary test window.



Figure 3.4. Screen shots of the live video feeds as presented on the main screen of choices: Outdoor enclosure (top left), indoor enclosure (top right), food preparation area (bottom left), and black screen (bottom right).

3.3.4 DATA COLLECTION

Using the video recordings of the 24 video choice sessions, each chimpanzee's visits to the area of the primary test window (where they were within reach of the touchscreen) were recorded and observed for the following behaviours and situations (see Tables 2.5 and 2.6): (1) The first touch to the touchscreen when the main screen is presented, (2) the video selected, (3) the location of the selected video, (4) whether or not the focal animal touched the touchscreen while the video was playing, and (5) whether or not the focal animal was near others (i.e. within one arms length of the focal animal).

3.3.5 DATA ANALYSIS

3.3.5.1 EVENT BEHAVIOURS

Event behaviours (Martin & Bateson, 2007) were calculated as a proportion of each individual's total behaviours in a given category and listed as percentages. For example, total correct touches were divided by the total frequency of correct and incorrect touches, and multiplied by 100. Proportions were used to allow for comparisons across individuals with different levels of interest in the research sessions where each individual contributed one data point per condition to avoid pseudo-replication of data (Dawkins, 2007). Two individuals (i.e. David and Ricky) were omitted from the analyses due to their limited involvement with the touchscreen monitor (> 3 minutes).

3.3.5.2 INTER-OBSERVER RELIABILITY

Inter-observer reliability (IOR) was tested between the primary researcher and a research assistant (SG) where the following behaviours (see Table 2.5) reached acceptable levels (i.e. $r > 0.7$ and $n \geq 5$) of reliability (Martin & Bateson, 2007): First touches: correct ($r = 0.93$, $n = 6$) and incorrect ($r = 0.97$, $n = 6$); video location: Q1 ($r = 0.96$, $n = 5$), Q2 ($r = 0.99$, $n = 0.7$), Q3 ($r = 1.0$, $n = 5$), and Q4 ($r = 0.99$, $n = 7$); video selections: outside ($r = 0.98$, $n = 7$), inside ($r = 0.99$, $n = 5$), food preparation area ($r = 1.0$, $n = 6$), and black screen ($r = 0.99$, $n = 6$); touches while video is playing: yes ($r = 0.99$, $n = 7$) and no ($r = 0.89$, $n = 7$); social context: alone ($r = 0.98$, $n = 7$) and near others ($r = 0.99$, $n = 5$).

3.4 RESULTS

3.4.1 ANALYSIS 1: INTEREST IN RESEARCH

The total time each chimpanzee spent within reach of the touchscreen (e.g. interacting with the monitor or observing) varied across individuals (see Table 3.1) ranging from 18 seconds (David) to 252 minutes (Cindy).

3.4.2 ANALYSIS 2: PERFORMANCE

After one year of participating in activities in the Research Pods, with three months dedicated to touchscreen training, (a) four chimpanzees (Cindy, Emma, Liberius, and Louis) correctly performed over 70% of first touches to the touchscreen monitor following the prompt of the main screen (see Table 3.1).

Table 3.1. Interest in research sessions (duration in minutes) and performance (correct first touch when prompted by the main screen of choices) during the video choices study.

	Duration (minutes)	Correct first touch
Cindy	252.28	92.50%
Liberius	84.84	71.95%
Kilimi	55.55	59.67%
Louis	41.58	80.52%
Lucy	38.84	12.50%
Kindia	17.60	0.00%
Emma	14.16	77.78%
Lyndsey	5.56	25.00%
Qafzeh	3.58	50.00%
Ricky*	1.13	--
David*	0.29	--

Note: An asterisk (*) indicates individuals who were omitted from analyses due to low interest in the research sessions.

When comparing (b) touches to the monitor before being prompted by the main screen (i.e. while a video was playing), for the individuals who reached 70% accuracy when activating videos with their first touch to the touchscreen, a t-test failed to reveal a statistically reliable difference between the mean number of correctly performed trials (i.e. waiting for the main screen of choices before touching the touchscreen) and chance at 50% (mean 61.18%, SE mean = 9.49%; One-sample T-test, $t(3) = 1.178$, $r = 0.56$, $p = 0.324$, see Figure 3.5).

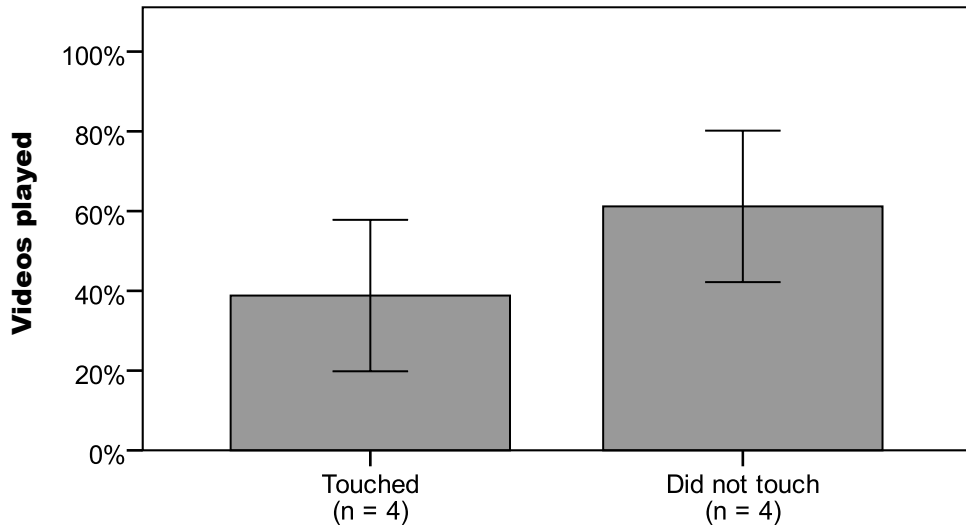


Figure 3.5. A comparison of the mean (\pm 1 SE) percentage of videos played where chimpanzees touched and did not touch the monitor before being prompted by the main screen.

3.4.3 ANALYSIS 3: VIDEO CHOICES

(a) For the chimpanzees who reached criterion by correctly activating the videos with their first touch to the touchscreen, one-sample t-tests failed to reveal statistically reliable differences between the mean number of video activations for each live-video feed and chance at 25% (Outside: mean = 24.00%, SE mean = 3.63%, $t(3) = -0.27$, $r = 0.16$, $p = 0.80$; Inside: mean = 23.37%, SE mean = 4.60%, $t(3) = -0.35$, $r = 0.20$, $p = 0.75$; Food preparation area: mean = 20.75%, SE mean = 5.92%, $t(3) = -0.72$, $r = 0.38$, $p = 0.52$; Black screen: mean = 31.88%, SE mean = 4.89%, $t(3) = 1.407$, $r = 0.63$, $p = 0.25$; see Figure 3.6).

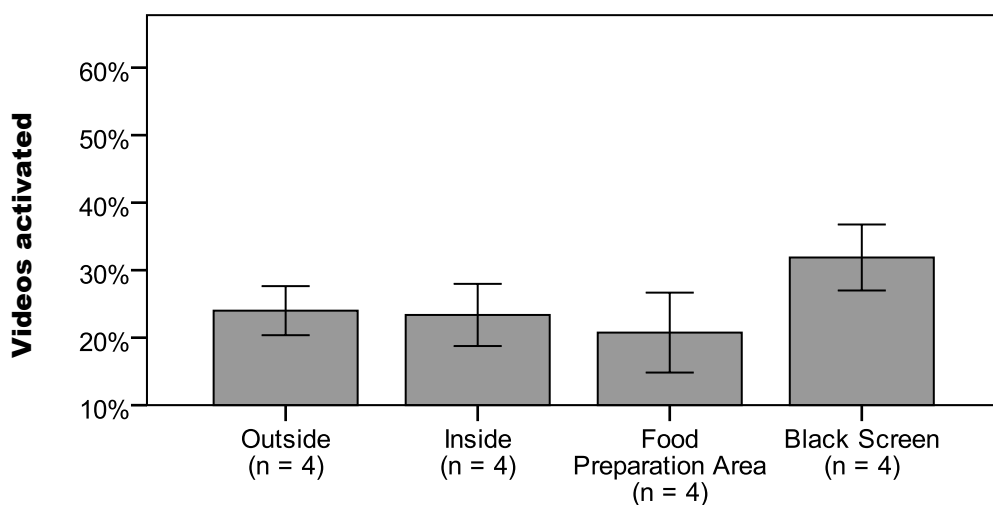


Figure 3.6. A comparison of the mean (\pm 1 SE) percentage of times each video feed was activated.

(b) For the chimpanzees who reached criterion, one-sample t-tests revealed a statistically reliable difference between the mean number of video activations for one video location and chance at 25% (Q1: mean = 22.29%, SE mean = 12.22%, $t(3) = -0.22$, $r = 0.13$, $p = 0.84$; Q2: mean = 56.17%, SE mean = 10.28%, $t(3) = 3.03$, $r = 0.87$, $p = 0.056$; Q3: mean = 2.94%, SE mean = 0.87%, $t(3) = -25.22$, $r = 0.99$, $p < 0.001$; Q4: mean = 18.60%, SE mean = 6.97%, $t(3) = -0.918$, $r = 0.47$, $p = 0.43$; see Figure 3.7). Q3 was selected significantly less than chance.

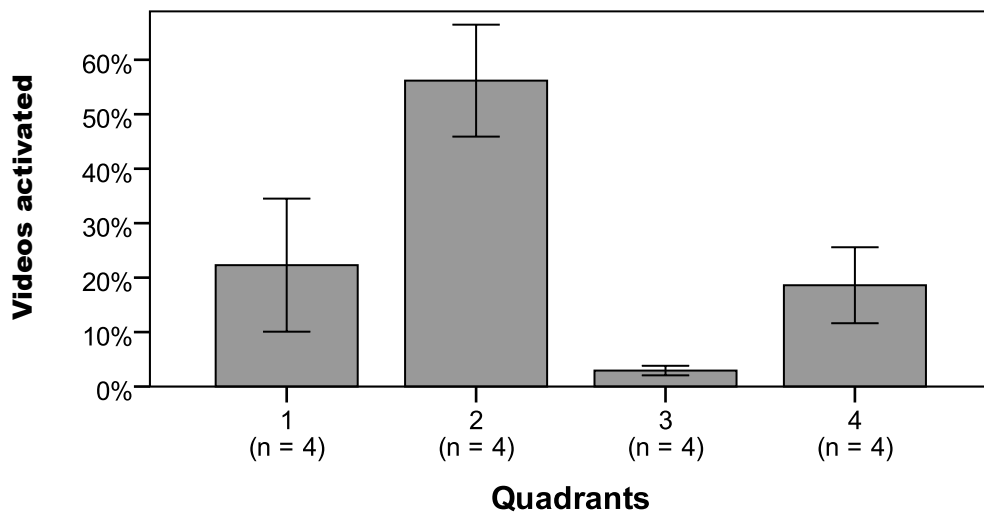


Figure 3.7. A comparison of the mean (\pm 1 SE) percentage of videos activated in each touchscreen quadrant (see Section 3.3.4.3).

3.4.4 ANALYSIS 4: GROUP TESTING

For the individuals who reached criterion, the presence of others (a) did not impact their ability to access the touchscreen. The proportion of total visits to the monitor where no videos were activated by the focal animal (transformed, $\log+1$) when alone (mean = 2.77%, SE mean = 2.24%) versus near others (mean = 20.66%, SE mean = 12.09%) did not significantly differ (T-test, $t(3) = -0.55$, $r = 0.30$, $p = 0.22$, $n = 4$, see Figure 3.8). This also applied to the individuals who did not reach 70% accuracy (transformed, $\log+1$; Alone: mean = 6.28%, SE mean = 3.84%; Near others: mean = 27.63%, SE mean = 7.75%; T-test, $t(8) = -2.68$, $r = 0.69$, $p = 0.03$, $n = 5$).

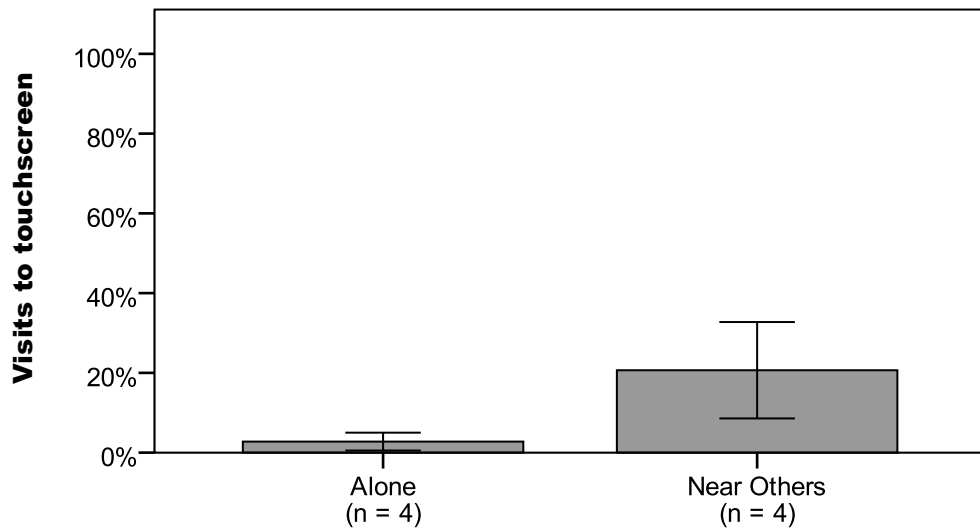


Figure 3.8. A comparison of the mean (\pm 1 SE) percentage of visits to the touchscreen monitor where the focal animal was alone or near others and did not activate any videos.

The presence of others (b) did not impact accuracy in using the touchscreen. Following Analysis 2 (Section 3.4.2), correct first touches did not significantly differ when individuals were alone (mean = 77.87%, SE mean = 6.90%) compared to when they were near others (mean = 86.43%, SE mean = 4.21%; T-test, $t(3) = -8.56$, $r = 0.98$, $p = 0.44$, see Figure 3.9). This also applied to the individuals who did not reach 70% accuracy (Alone: median = 50.00%, Near others: median = 0.00%, Wilcoxon signed-ranks test, $T < 0.01$, $r = -0.51$, $p = 0.11$, $n = 5$).

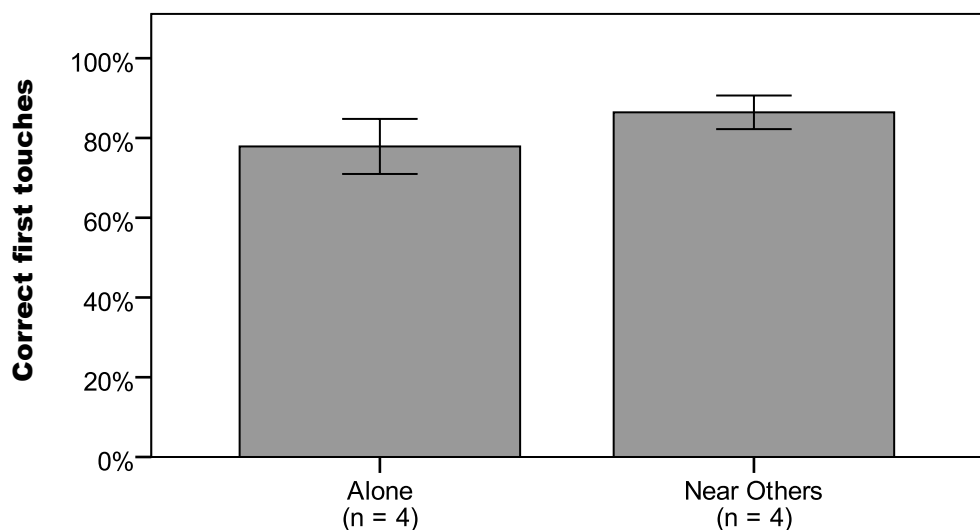


Figure 3.9. A comparison of the mean (\pm 1 SE) percentage of correct first touches to the touchscreen monitor when alone and near others.

3.4.5 SUMMARY OF RESULTS

Four analyses within this chapter addressed cognitive activities with research naïve chimpanzees where interest in the research sessions varied across individuals. When examining performance, four individuals correctly activated videos with their first touch to the touchscreen over 70% of the time (Cindy, Emma, Liberius, and Louis). Of those individuals, they did not use the touchscreen as intended: There was no statistical difference between the percentage of videos played where chimpanzees touched and did not touch the monitor before being prompted by the main screen of choices. The type of video feed did not impact selection, but the location of the video (i.e. which quadrant) did appear to matter, quadrant 3 (Q3) was selected significantly less than chance (25%). In terms of group testing, the presence of others did not impact access to the monitor nor accuracy of performance (for both those who performed with at least 70% accuracy and those who did not).

3.5 DISCUSSION

3.5.1 PERFORMANCE IN THE VIDEO CHOICE STUDY

The purpose of providing live video feeds to allow the chimpanzees to make selections about what they watched was to investigate their preferences through patterns in their selections. In order for this to be a valid concept, we needed to know if they understood the activity. Based on their performances, certain individuals could reliably activate videos by touching the targets, but there is no evidence that they consistently discriminated or preferred different content and once the videos were playing. It seemed that they did not understand the need to wait for the video to stop before making another choice.

This does not necessarily speak about the cognitive abilities of an older group of research-naïve chimpanzees, but instead points out differences in the perception of the activity's goal. The group's previous experience with training in the Research Pods, however limited, revolved around the concept of fairly fast-paced bouts of training where a task was followed by a reward and then repeated or adjusted. Often the tasks would build up where more than one response was required before a reward was delivered, but generally there was no delay between response and reward. We anticipated that in addition to a food reward, viewing a video would be rewarding in itself and capture their attention,

however, contrary to previous research (Bloomsmith et al., 1990; Bloomsmith & Lambeth, 2000), this was not the case. This group of chimpanzees was not particularly interested in the video feeds and subsequently continued to try to earn rewards by doing what they learned early on in training: touch the screen to earn a reward. In Chapter 6 we discuss the reactions of the chimpanzees to passive viewing of video images in relation to group introductions where a few individuals from the Edinburgh group (those included in this study) showed occasional interest in the video, whereas the Beekse Bergen group (the new group) showed a great deal of interest in video; perhaps due to previous exposure, although the extent of their experience is not known in any detail.

3.5.2 VIDEO CHOICES

The selection of videos did not seem to rely on the content of the feeds themselves, but rather on the location of the video within the touchscreen's quadrants. While each chimpanzee exhibited their own location preferences, possibly based on the length of their arms (e.g. Liberius, who has the longest arms of the group, was able to sit on the side of the touchscreen near the food chute while easily reaching Q1, whereas Cindy, a smaller chimp, often relied on Q2 and Q4), the group generally preferred Q2, most likely because it is the quadrant closest to the food chute and at eye level.

Holding group sessions, where the content of the live feeds relied upon the chimpanzees within the group to be distributed throughout the enclosure (to be viewed on camera) rather than in the Research Pods themselves, could have been problematic and possibly explained the lack of video-feed interest. Another reason why there was no preference for any particular video feed might have been because the study relied on only the visual modality. An element that differentiated our video feeds from much of the previous research was the removal of sound. By removing sound, we hoped to isolate any interest in the visual aspect of videos themselves. Instead this might have been part of the problem and a linking factor that has drawn other chimpanzees to show an interest in video. Chimpanzee communication is often multimodal (Slocombe et al., 2011) and seems to be very important in attracting chimpanzee attention to visual images (S. Vick and R. Mayeri, personal communication, 2011). Future research might incorporate sound, assess interest in video prior to conducting this sort of study, or ensure that a longer and more intensive training period could be dedicated to the study.

3.5.3 CHALLENGES IN GROUP TESTING

Group testing is a concern within the field of animal behaviour (Schapiro et al., 2003), however, in this study, the presence of others did not impact upon the chimpanzees' ability to access the test window. While those who are familiar with chimpanzees might expect multiple individuals using a single food-reward apparatus to be problematic, the multiple-trainer approach to disperse and occupy individuals, seemed to be effective in reducing competition, but may not be practical in other research contexts. Even though group testing did not prove to be problematic for this groups' access to the touchscreen monitor, when two or more individuals were in front of a test window, it presented a challenge for the assessment of individual cognitive abilities. Filming activities at the test window became increasingly difficult as more chimpanzees tried to participate in the tasks (see Figures 3.12 - 3.14). However, this should not be a deterrent from hosting group sessions, as previously mentioned, having additional trainers in place in other training locations (i.e. the other test windows) can distract the majority of the chimpanzees in order to allow specific individuals to focus on the testing apparatus.

In a different approach to minimising competition-related behaviour within a research context, Perdue et al. (2011) relocated their touchscreen from an indoor to an outdoor enclosure, where their orangutans could access the apparatus in a complex environment with potential distractions from other activities on offer. This method worked for their group of four orangutans, but with potential species differences (e.g. temperament), whether or not it would work as well with a larger group of chimpanzees remains to be seen.

While the social environment sometimes dictated whether or not individuals could access the monitor, it did not impact their performance. While this finding would be more powerful if it were proven that the chimpanzees had a full understanding of the task we intended, it nonetheless showed that this group performed the same way regardless of the presence of others. While limitations in access and use from the presence of others could have constrained their ability to learn (see Chapter 4 for analyses on the impact of social dynamics on behaviour during training and testing), the opportunity to watch

others interact with the monitor could have led to social learning². Perhaps training one chimpanzee to serve as a demonstrator for the rest of the group (i.e. Subiaul et al., 2004; Whiten et al., 2005) would be an alternative strategy for future research.

There are positive and negative aspects of conducting cognitive research with research-naïve chimpanzees. The ability to work with a chimpanzee group who is not biased by previous research experience is unusual. However, with the perk of catching a glimpse of how they see the world, comes the challenge of helping them understand how to participate in the activities provided. Progress may be slow dependent upon group dynamics and practical considerations (e.g. priorities of animal management etc.). A group testing environment is encouraged to benefit from early training stages when working with research- and training-naïve chimpanzees.

² Anecdotally speaking, Lucy, the chimpanzee who participated the most in the research sessions (see Chapter 4), often participated as an observer. We believe the initial benefit to her was the opportunity to steal or find any food rewards left behind, but after minimal interaction with the touchscreen during the training period, towards the end of the video choices study, based on watching others, she appeared to understand what she needed to do with the touchscreen to earn the food reward.



Figure 3.12. One chimpanzee participating at the test window.



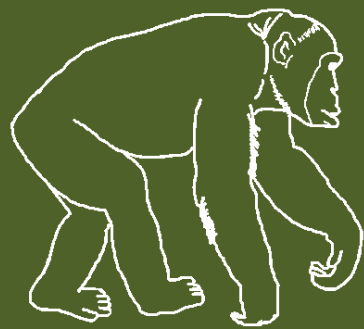
Figure 3.13. Two chimpanzees participating at the test window.



Figure 3.14. Three chimpanzees participating at the test window.

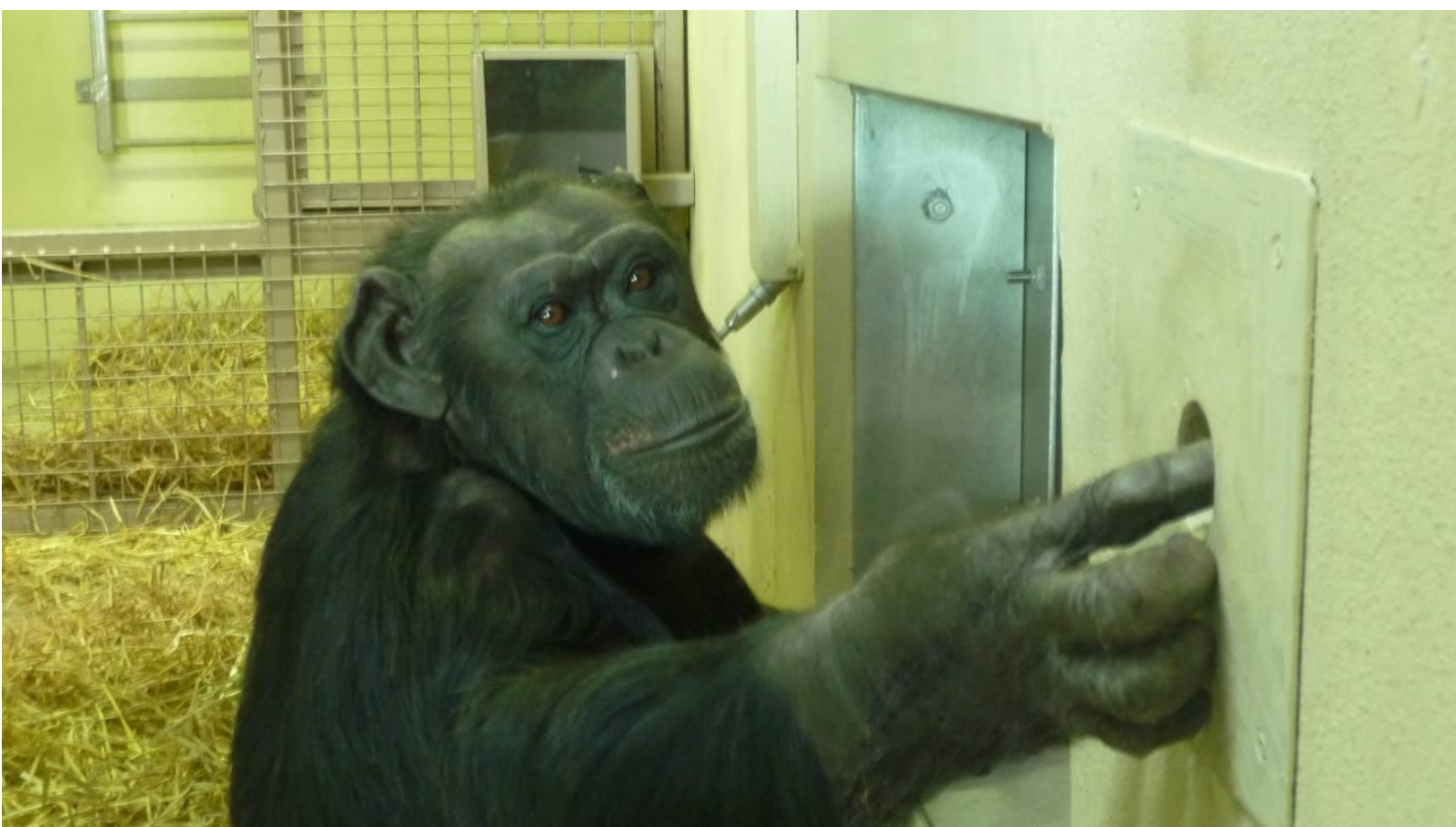
3.6 SUMMARY AND CONCLUSIONS

The challenges overcome during the initial stages of developing this research programme created an environment that both allowed and required flexibility from the researcher, the care staff, and the chimpanzees. Ultimately, we were not able to learn about chimpanzee preferences in watching live-video feeds, which essentially involved visually eavesdropping on the rest of their enclosure. However, we were able to shed some light on a few of the issues in the group testing debate. While the presence of others impacted the ability to access the testing apparatus, it did not affect accuracy. If the individuals are interested in participating at the same time, a system where additional trainers can distract surplus individuals with activities at another test window can alleviate the pressure of participation at the primary test window. The addition of this study to the research literature will, perhaps, provide researchers and animal care staff with additional information to support the idea of conducting research in a group environment.



CHAPTER 4

WELFARE ASSESSMENT DURING THE DEVELOPMENT OF A COGNITIVE RESEARCH PROGRAMME



WELFARE ASSESSMENT DURING THE DEVELOPMENT OF A COGNITIVE RESEARCH PROGRAMME

4.1 ABSTRACT

This research project aimed to develop a chimpanzee (*Pan troglodytes*) cognitive research programme with the use of video cameras and computerised testing. The goal of the current study was to identify whether or not the introduction of this research programme had any impact on chimpanzee welfare. Specifically, whether higher rates of self-directed behaviours (SDBs) were observed, as would be expected if the chimpanzees were anxious, uncertain, or frustrated by the training and testing, compared to other activities. The SDBs of 11 chimpanzees (six males; five females) were collected over a 16 month period and compared across conditions: (1) baseline (non-training/research situations) and (2) an ongoing, two-year programme of husbandry training (off-exhibit, i.e. chimpanzees were requested to station/stay while being closed into an area) and (3) training and research for cognitive testing (i.e. introducing new on-exhibit research areas and targeting to shape touchscreen use). Findings indicated that there was no significant difference between conditions for the six chimpanzees who were present during all phases of the research project. SDBs during the different phases of research did not differ, except for a difference between the Husbandry Training and Baseline condition during the Initial Training phase, where SDBs were higher during Husbandry Training. Additionally, the rates of SDBs were examined in relation to the specific characteristics of cognitive training and testing: social context, reward contingency, visual access to keepers, and differences in levels of research session interest. For social context, we also recorded vigilance to assess levels of social monitoring. Only visual access to keepers impacted on rates of SDBs; these increased when visual access was restricted during research training and testing. Social monitoring did not differ in relation to social context or rank. Females were more interested in the research sessions than males, however no relationships were found between level of interest and rates of SDBs, rank, or disruptions within the group (i.e. large-scale displays or fights). Overall, the introduction of a cognitive research programme did not compromise welfare, and the chimpanzees' repeated interest suggests that the research was reinforcing.

4.2 INTRODUCTION

4.2.1 THE POTENTIAL IMPACT OF COGNITIVE CHALLENGE ON WELFARE

Despite a recent explosion in cognitive programmes within the zoo context (see Section 1.2.2), there has been limited attention to the potential welfare implications of these developments. As living in captivity can easily lead to boredom due to limitations in space, available activities, and group size and overall dependency on keepers, incorporating mentally stimulating challenges that can be reasonably solved with the tools an animal has (including mental abilities), can be beneficial, at least when the challenge provides the animal with a choice to participate and control over the outcome (Meehan & Mench, 2007). Choices provide a way in which animals can exhibit their preferences and feel in control of their environment (Badihi, 2006). While both are notably restricted in captivity, it is important to supply it in as many ways as possible to enable animals to make decisions for themselves (Markowitz, 1982, as cited in Badihi, 2006; Laule & Desmond, 1998; Markowitz & Aday, 1998; Poole, 1998), albeit within species-typical social constraints, such as age and dominance rank.

Cognitive research is potentially a means of environmental enrichment (Platt & Novak, 1997; Bloomsmith et al., 2000; Ross et al., 2000), that is, “an animal husbandry principle that seeks to enhance the quality of captive animal care by identifying and providing the environmental stimuli necessary for optimal psychological and physiological wellbeing” (Shepherdson, 1998, p1). Primates, particularly chimpanzees, are curious beings and are generally interested in novel items or activities (Paquette & Prescott, 1988), which is why cognitive tasks are particularly important as they allow for different challenges over time to avoid habituation (Tarou, 2004). However, with any novel situation in a captive animal’s life, such as husbandry training and cognitive testing, an animal’s initial reaction is likely to be one of uncertainty. This also highlights a need to monitor behaviours in response to the task type or stimuli and to be aware of how individuals cope with new or challenging situations, in order to validate the inclusion of the stimuli in the animal’s life. Individual variation in response to challenges is expected (Herrmann et al., 2010). If certain activities incur too high usage, it might be beneficial to withdraw or limit usage. While the goal is to offer challenge, it is crucial that this is not to the detriment of other species-typical activities.

In addition to the anticipated challenges from working with animals, researchers must take the zoo environment into consideration (Hosey, 2005). When working with animals on public display there is the potential for visitor effects to influence behaviour (Hosey & Druck, 1987; Mitchell et al., 1992; Wood, 1998) and also for the research to influence public perception (see Chapter 5). The concept of holding research on public display holds great opportunities to engage the public with science, but visitor noise and activities can impact upon primate behaviour and welfare (Hosey, 2005). Comparisons of behaviour during activities conducted on display and off display (behind the scenes) will help shed light on the implications of allowing visitors to get a glimpse into ongoing research activities.

Although there is an implicit assumption that cognitive tasks serve as environmental enrichment, especially in species with complex cognitive abilities, there has been relatively little systematic study of the welfare implications. There is now a growing awareness of the need to also focus on the potential welfare implications of cognitive testing within a zoo context (Wagner & Ross, 2008; Ross, 2010; Perdue et al., 2011). In any research context, ensuring that the study is as stress-free as possible is important for both the welfare of the animal and the quality of the research (Joint Working Group on Refinement, 2009; Poole, 1997; Reinhardt, 2004; Rennie & Buchanan-Smith, 2006b). Evaluating the internal state of non-verbal animals is challenging, but important to our understanding of their wellbeing and quality of life (Novak & Suomi, 1988; Novak & Petto, 1991; Shepherdson, 1998). Without being able to directly ask the subject, researchers must develop methods to analyse behaviour and try to assess these non-tangible, mental states (Rosenblum, 1991; Maestripietri et al., 1992).

4.2.2 SDBS AS A MEASURE OF WELFARE IN CHIMPANZEES

By providing animals with the choice to engage in an activity and exhibit their preference, researchers may partly assess welfare directly from the animals' responses (Dawkins, 1983). Performance assessment aside, if an animal chooses to attend or participate in a research session instead of engaging in other available activities (i.e. foraging, grooming others, etc.), it indicates that these sessions are of interest to the animal. The degree to which an individual is interested in an activity could be assessed by the individual's proximity to the activity. In a group training and testing environment, even if an individual is not directly participating in the activity, they still might learn about the activity by observing

others (Prescott & Buchanan-Smith, 1999; Whiten, 2000; Matsuzawa, 2002; Savastano et al., 2003; Subiaul et al., 2004), an important consideration within group training and testing. However, usage should be monitored; if learning and performance on tasks remain low over time, the underlying motivational factors for participation should be reconsidered.

While repeated interest and willingness to participate are quantifiable categories that can be helpful in determining whether or not an activity is enriching and mentally stimulating, additional behaviours should be enlisted to assess welfare. Perhaps the most obvious behavioural concerns would be aggression or stereotypies. Mixed reactions have been seen in response to the addition of a video apparatus; for example, there was no increase in aggression in rhesus macaques (Platt & Novak, 1997), nor orangutans (Perdue et al., 2011), however, an increase in aggression has been seen in the orangutans from Perdue et al. (2011) in a previous study where the apparatus was in an indoor space (Tarou, 2004). While monitoring these behaviours is important, there are more subtle measures that indicate levels of uncertainty (i.e. self directed behaviours) when assessing an immediate response to environmental stimuli.

Past research on behavioural indicators of wellbeing has primarily concentrated on SDBs as a conflict between two motivational drives (Tinbergen, 1952). These are behaviours that are within the species-typical repertoire but often occur out of context from their expected function or at higher than usual rates, for example, chimpanzee scratching (as reviewed by Maestripietri et al., 1992). Also known as displacement behaviours, SDBs are suggested to be an unconscious redirection of behaviour, often due to anxiety-inducing situations where the animal is uncertain about how to behave (Maestripietri et al., 1992). The empirical study of SDBs in primates and their potential value as a measure in applied contexts was largely neglected until the early 1990s (te Boekhorst et al., 1991; Troisi et al., 1990), but has now been applied in field and captive settings to explore arousal in chimpanzees (Captive studies: Aureli & de Waal, 1997; Baker & Aureli, 1997; Leavens et al., 2001; Troisi, 2002; Field studies: Itakura, 1993; Castles et al., 1999; Kutsukake, 2003a; Hockings, 2007).

SDBs are used to assess states of uncertainty that are often associated with anxiety-related behaviour (Baker & Aureli, 1997; Bassett et al., 2003; Hopkins et al., 2006; Kutsukake, 2003a). SDBs occur in many

forms and include scratching, rubbing, self grooming, and yawning (Maestriperi et al., 1992; Aureli & de Waal, 1997; Baker & Aureli, 1997; Diezinger & Anderson, 1986; Troisi et al., 1991). Examples of these behaviours are shown in Figures 4.1 – 4.4. Scratching in particular has been often explored within *in situ* and *ex situ* environments (Baker & Aureli, 1997; Kutsukake, 2003a; Leavens et al., 2004; Hockings, 2007) as two separate types, gentle and rough, where gentle scratches are suggested to be a displacement behaviour and rough scratches are suggested to be a more intense form of arousal possibly indicating anxiety (as reviewed by Baker & Aureli, 1996).

Given the difficulty in identifying whether or not an animal is scratching because he/she has an itch or for other hygiene reasons, perhaps it is more appropriate to say that the behaviours are informative when there is a change in rate rather than looking at the absolute rate alone. However, establishing a species-typical rate for SDBs, to serve as a baseline, is challenging as there is variance within and between contexts (see Table 4.1) and definitions (Baker & Aureli, 1996; Leavens et al., 2001; Hopkins et al., 2006). SDBs are considered to be valid measures of arousal in non-human primates due to a negative correlation between behavioural measures (e.g. scratching) and biological intervention (e.g. the administration of anti-anxiety medications) as reviewed by Troisi (2002). In several cognitive testing situations, SDBs are affected by the level of difficulty in cognitive tasks, with rates increasing with the level of challenge (Itakura, 1993; Leavens et al., 2001). These findings support the use of SDBs as indicators of uncertainty in response to challenge.

Table 4.1. Scratching rates (mean rate per minute) from previous studies with chimpanzees in the wild and group housed in captivity.

Author	Condition	Scratching (mean rate per minute)
Leavens et al., 2004	Laboratory	0.60*
Baker & Aureli, 1997	Laboratory	0.28
Kutsukake, 2003a	Wild	0.84^
Hockings, 2007	Wild	0.15^

Note: Rates are estimations with slight adjustments to allow comparison between data collection methods. All rates are from a baseline condition with the exception of Leavens et al., 2004, marked with an asterisk (*), which is in the context of cognitive testing. A caret (^) denotes only rough self scratches are represented in the data.



Figure 4.1. An example of scratching by Kindia (right), with Qafzeh nearby (left).

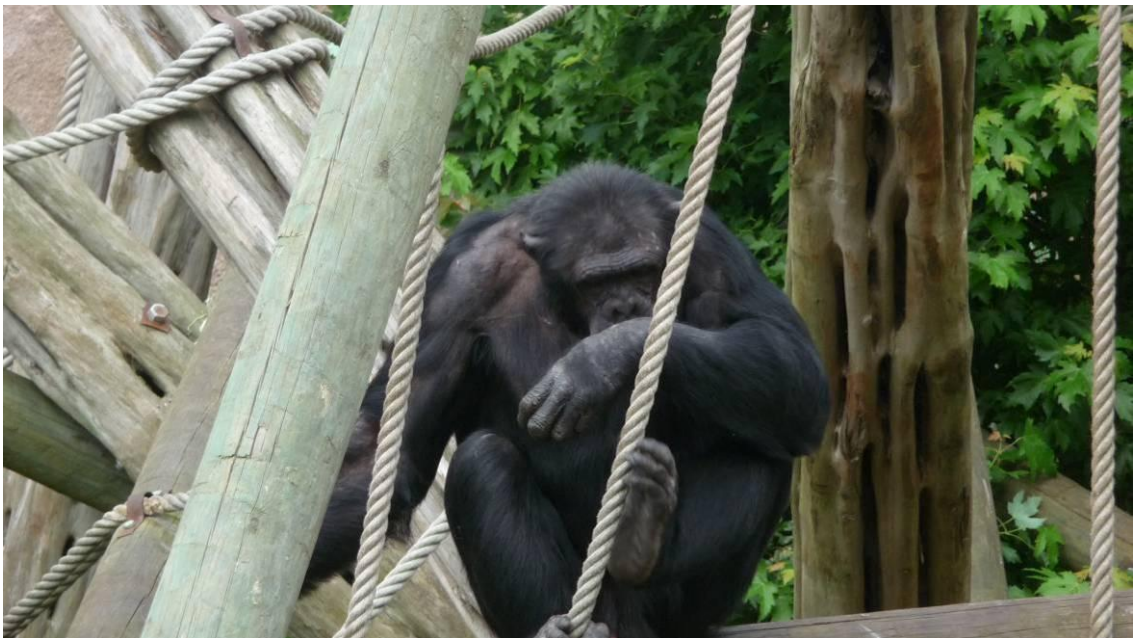


Figure 4.2. An example of rubbing by Qafzeh.



Figure 4.3. An example of self grooming by Kindia.

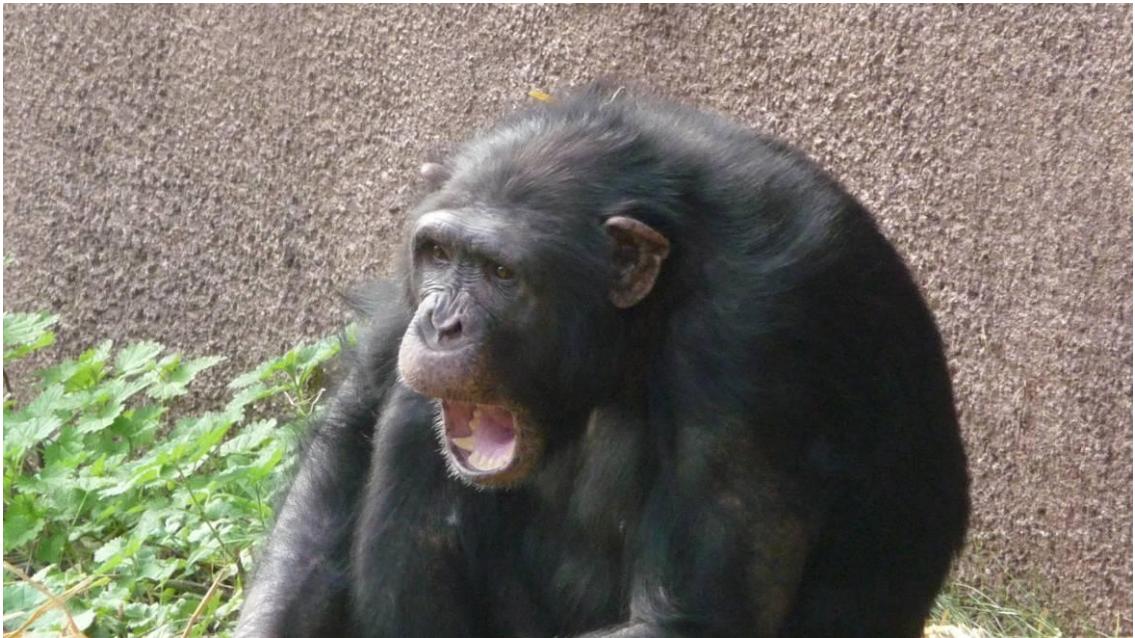


Figure 4.4. An example of yawning by Liberius.

4.2.3 IMPACT OF SOCIAL FACTORS AND PREDICTABILITY DURING COGNITIVE TASKS

In the current study, free access to the Research Pods during sessions and group testing, meant that social factors were also likely to have an impact upon participation and uncertainty, as indicated by SDBs (Baker & Aureli, 1997). Vigilance is a potential measure of uncertainty that has not received as much attention as SDBs. While primarily studied in relation to the monitoring of predation threats (Treves, 2000; Kutsukake, 2007), vigilance also allows conspecifics to be monitored, with the most attention being directed towards more dominant animals (Chance, 1967). Contrary to the concept that vigilance reduces as group size increases (as reviewed by Pulliam, 1973), Kutsukake (2003b & 2007) reported that vigilance durations in wild chimpanzees increased when group members were in close proximity, suggesting that individuals were vigilant towards their group members, particularly within competitive contexts.

Monitoring vigilance during research sessions allows the assessment of how much attention is allocated away from the training and testing tasks to attend to social dynamics. Beyond anecdotal data noting that in mandrills (*Mandrillus sphinx*), dominant animals were more distracted by the need to monitor the group outside of the testing facility during research sessions (Leighty et al., 2011), vigilance behaviour has yet to be systematically studied in the cognitive research setting. This study is the first quantitative analysis of vigilance behaviour in a cognitive training and testing environment.

Social factors may not only impact upon vigilance but also influence participation and performance. Research examining sex differences in the development of cognitive tasks suggest that female chimpanzees tend to perform better on cognitive tasks than male chimpanzees because males are likely to focus their attention on dominance relationships (Lonsdorf, 2005). However, anecdotal data from Leighty et al. (2011) suggest that social hierarchy and dominance relationships affected three dominant ranking animals, two of which were female. With these conflicting points in mind, it is important to empirically assess the relationship that rank and sex have on participation and interest in cognitive tasks in a group context. In addition to investigating the impact of the general training and testing conditions, two additional factors of interest within the methodology were identified during the project and examined in more detail. These factors could potentially impact uncertainty and be reflected in changes

in the rates of SDBs: (1) providing visual access to keepers during training and testing situations; (2) delivery of food rewards being contingent upon chimpanzee actions.

Interactions between animals and keepers/researchers usually rely on visual feedback enabling both parties to interpret behaviour (as shown in training methods from Pryor (1999) and Ramirez (1999)). For a social animal like the chimpanzee, being able to visually interact with keepers during activities can help to form trusting relationships by increasing predictability, allowing for anticipation, and facilitating greater behavioural synchrony, for example, indicators that a behaviour is correct and thereby bridging the delay until the contingent food reward is delivered. The group's previous experience with training was limited to the recent start of a husbandry training programme (approximately 6 months prior to the start of the project) that centred on interaction with the keepers. As one aspect of the project was computerised, it was important to monitor how this change (removal of visual access to keepers during training and testing to allow chimpanzees to focus on tasks rather than keeper activity) might impact welfare.

Predictability plays a key role in the welfare of captive animals as environmental complexity is negatively correlated to predictability, particularly when it comes to feeding times (Bassett & Buchanan-Smith, 2007). While highly predictable feeding routines can lead to undesirable anticipatory behaviours (Bloomsmitth & Lambeth, 1995; Waitt & Buchanan-Smith, 2001), other forms of high predictability can positively enhance welfare, particularly through the use of reliable signals and behavioural markers as a means to communicate during positive reinforcement training (Pomerantz & Terkel, 2009). If animals have a semblance of control (by making choices based on signals or other decision making activities) within their managed lifestyles, welfare will be enhanced (Sambrook & Buchanan-Smith, 1997; Badihi, 2006). It is in this sense that having (and understanding) a relationship between one's actions and the delivery of a food reward (i.e. contingent rewards) might impact the rates of SDBs; contingent rewards are predictable and provide opportunities for chimpanzees to exert some control.

4.2.4 STUDY AIMS

Research in zoological settings is now starting to focus on cognitive studies in relation to welfare (as reviewed by Ross, 2010; Perdue, 2011), but there are still few reports available. This study aimed to

assess welfare during the development of a cognitive research programme by examining participation, SDBs, and vigilance across three conditions (off-exhibit Husbandry Training, on-exhibit Research Pod Activities, and a Baseline condition when no training was offered, see Table 4.2). These concepts were explored in seven analytical categories in which we identified the following hypotheses:

ANALYSIS 1: ADDITION OF A COGNITIVE RESEARCH PROGRAMME

(a) SDBs would occur at a higher rate during training and testing conditions compared to the Baseline and Husbandry Training conditions (specifically that the challenge of the new Research Pod Activities would prompt higher rates of SDBs than the Husbandry training activities (activities the chimpanzees were familiar with), and both Research Pod and Husbandry training activities would prompt higher rates than the Baseline, no training, condition).

(b) SDBs would occur at a higher rate as research activities became novel or increased in difficulty; specifically, rates would be lower during Initial Training than Self Recognition testing, which would be lower than the Touchscreen Tasks phase. As Self Recognition and Touchscreen Tasks were both novel for the group, it was expected that these phases would have higher rates of SDBs than Initial Training.

ANALYSIS 2: GROUP TRAINING AND TESTING

(a) SDBs would occur at a lower rate and (b) vigilance towards the Research Pod entrance would occur at a higher rate when participants were alone compared to when they were nearby conspecifics (i.e. within one arms-length).

ANALYSIS 3: CASE STUDY: GROUP TRAINING

(a) SDBs and (b) vigilance would occur at a lower rate during individual sessions (i.e. training with Cindy, when conspecifics could not physically enter the Research Pods) compared to during group sessions.

ANALYSIS 4: VIGILANCE

(a) Higher ranking members of the group would exhibit more vigilance behaviours (i.e. looking towards the entrances to the Research Pods) than lower ranking members.

ANALYSIS 5: REWARD CONTINGENCY

(a) SDB rates would be higher when rewards were not contingent upon chimpanzee activity compared to when rewards were contingent upon chimpanzee activity.

ANALYSIS 6: VISUAL ACCESS TO KEEPERS

(a) SDBs would occur at a higher rate when visual access to keepers was blocked compared to when chimpanzees had full visual access to their keepers during training and testing.

ANALYSIS 7: PARTICIPATION

(a) Those who had the most interest in the research sessions would have the lowest rates of SDBs.

(b) Females would have more interest in research sessions than males.

(c) Low-ranking chimpanzees would have more interest in research sessions than high-ranking chimpanzees.

(d) Interest in research sessions would decrease as disruptions from the group (displays and fights) increased.

4.3 METHODS

4.3.1 STUDY ANIMALS

The study animals were 11 chimpanzees (*Pan troglodytes*) from the Edinburgh group, 6 males and 5 females ranging in age from 9 to 47 years old (mean 26.36, \pm S.E. 12.75) at the onset of the project in May 2008 (additional information on the group, their management, and housing conditions is described in Chapter 2, General Methods).

4.3.2 APPARATUS

Noldus Observer XT 8.0 software and paper checksheets (see Appendix B2 and B3) were used to record instances of SDBs, vigilance, and interest in research. A Sony HD 3CMOS colour video camera was used to video tape Research Pod sessions, which were reviewed using QuickTime Player 7.6.4 on a Toshiba Satellite Pro U400 computer.

4.3.3 RESEARCH DESIGN

Three phases within the development of a cognitive research program (Initial Training, Self recognition, and Touchscreen Tasks, see Table 4.3 and Figures 4.5 – 4.9) were used in the comparison of welfare-related behaviours across three conditions: (1) baseline (non-training/research situations); (2) husbandry training; and (3) training and research for cognitive testing. Baseline behaviours and an ongoing, two year programme of husbandry training (held off-exhibit) were used to compare behaviours exhibited during everyday activities to the behaviours exhibited during the development of the cognitive research programme.

Keepers offered the husbandry training on a daily basis to the group where individuals were trained to station/stay while being closed into an area for animal management purposes. Similarly, prior to the introduction of computerized activities, the research naïve chimpanzees were habituated to the research facilities during initial training (7-month period); they were encouraged to voluntarily enter the Research Pod areas, remain there for a reasonable amount of time, and participate in familiar forms of husbandry training (i.e. targeting) to earn food and verbal rewards. Following habituation, they were exposed to self-recognition stimuli (2-month period) and participated in touchscreen tasks (7-month period).

These research areas are on public view and visual access to the keepers is provided through test windows. When computer based tasks were introduced, the touchscreen blocked the test window, which meant that the keepers were no longer visible. Cameras placed in chimpanzee-proof boxes within the research area allowed behaviour to be monitored even when test windows were blocked. Training for husbandry training and research conditions were performed by the keepers and researcher.

Table 4.2. Details for the three conditions within the project: Husbandry Training, Research Pod Activities, and Baseline.

Condition	Definition	Observation Schedule	Observation Area
Husbandry Training	Ongoing programme (2 yrs) of PRT husbandry training offered daily (off-exhibit, i.e. station/stay while being closed into an area).	Group sessions were offered daily between 08:00 and 09:30 (approximately 3-5 minutes each). Observations were made up to 5 days per week.	Bed area (off exhibit).
Research Pod Activities	Research for cognitive testing (see Table 4.3).	Sessions ranging from 10-90 minutes were offered up to 4 times per week. Primary time frames were 11:30 to 13:00 or 14:00 – 15:30.	Research Pods (on exhibit).
Baseline	Observation of behaviour outside of training and research activities.	Two 10-minute observation sessions were conducted for each individual during each Research Pod activity phase (one AM and one PM).	Pods 1, 2, 3, and outside (on exhibit) and bed/tunnel area (off exhibit).

Table 4.3. Details for the Research Pod Activity phases: Initial Training, Self Recognition, and Touchscreen Tasks (see Figures 4.5 – 4.9).

Phase	Definition	Time period (months)	Sessions	Duration Mean \pm SE (mins)	Data coding
Initial Training	Encouraged the chimpanzees to become familiar with the Research Pods and activities offered (i.e. target to a ball at the test window).	7	125	14.33 \pm 0.85	Live
Self Recognition	Designed to allow the chimpanzees to test the relationship between their actions and image, first with a mirror and then with a computer monitor (live images from two angles).	3	12*	33.25 \pm 1.6	Video
Touchscreen Tasks	Making choices on a touchscreen monitor; 4 cameras fed live video to the monitor and if selected, one would appear in full screen for 10 seconds before reverting back to a main menu of choices for another selection.	5	56*	30.95 \pm 1.12	Video

Note: An asterisk (*) indicates the test phases where group sessions with basic activities from the Initial Training period were held between test session days to maintain chimpanzee interest in research activities: Self Recognition ($n = 31$), Touchscreen Tasks ($n = 12$).



Figure 4.5. Target training during the Initial Training phase of the Research Pod activities. In order to earn a reward, Cindy (right) must figure out the pattern that Keeper is presenting with the red and yellow balls. In this version, if Cindy touches the red ball wherever it appears in the window, she gets a reward. On another day, the correct stimulus might be the yellow ball.



Figure 4.6. Emma takes a closer look at herself during the mirror portion of the Self Recognition phase.



Figure 4.7. Cindy sees live-video footage (frontal camera) of herself during the monitor portion of the Self Recognition phase.



Figure 4.8. Cindy correctly touches the target on the monitor during the training portion of the Touchscreen Tasks phase.

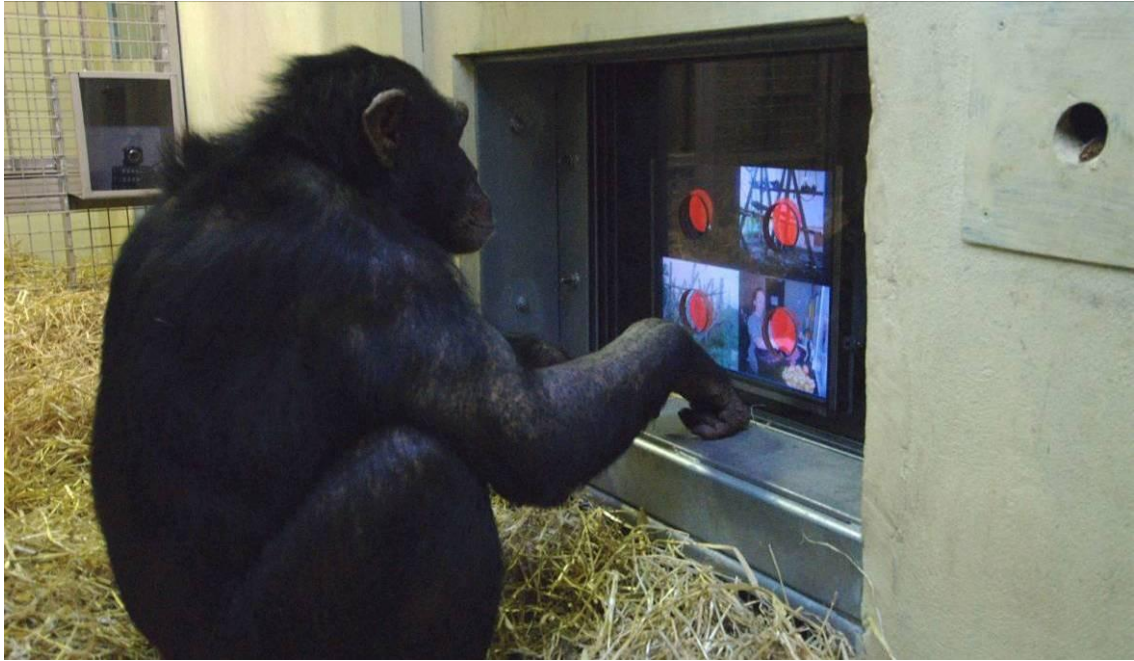


Figure 4.9. Liberius looking towards the monitor during the testing portion of the Touchscreen Tasks phase (photo ©Kevin Flay).

4.3.4 DATA COLLECTION

Data were collected and compared across three conditions (each with data from the timer period of each phase of research): Baseline, Husbandry Training, and Research Pod Activities (see Table 4.2 for details on conditions and observation schedule). Observations occurred over a 16-month period, from August 2008 – November 2009, in both on- and off-exhibit areas to cover the three phases of research. The distribution of observation periods across phases was constrained by animal management issues and researcher availability. Data were collected as uniformly as possible across all phases of research, but in the interest of training progress, if the chimpanzees seemed ready to move onto the next phase of the research, they were not held back.

Focal sampling was used to record all-occurrences of SDBs and vigilance behaviour (see Table 2.5), as these are behaviour events that are short in duration and not suited to instantaneous time sampling (Martin & Bateson, 2007). Scratching, one of the most frequently occurring SDBs and an easily identifiable behavioural measure (Maestriperi et al., 1992), is primarily performed in two ways: gentle (movements of the hands and fingers with no arm movements) and rough (movements of the hands and fingers with arm movements) (Baker & Aureli, 1997). However, due to the low frequency of

occurrence of gentle scratches, and in accordance with previous research (Leavens et al., 2001; Hopkins et al., 2006), scratching behaviours were collapsed into a single category, referred to as scratching.

At the same time, instantaneous time sampling was used to record longer duration states, including where each chimpanzee was located in the Research Pods (30s intervals; see Table 4.4). Observation sessions were coded in real time with the exception of two phases of the Research Pod Activities condition that were coded from video for logistical reasons (Self Recognition and Touchscreen Tasks).

Regardless of the phase, scan sampling of chimpanzee presence was always recorded in real time.

Individuals were numerically ranked into three categories (high, middle, and low) based on qualitative assessments from the researcher and three keepers who worked with the chimpanzees they ranked for at least one year (see Table 2.2 and Appendix A1) through observations of aggression, submission, priority access to areas, and support received during fights.

Focal animals were observed during live coding sessions (see Table 4.3) as often as possible when Husbandry Training and Research Pod Activities were offered. To accommodate differences in session lengths a total of three minutes of data for each chimpanzee were used in the analysis (see Appendix C1). Focal animals were selected based on the following qualifications: (1) The first chimpanzee to enter the Observation Area (see Table 4.2) was the first focal animal. (2) If the first chimpanzee had already been observed, the second chimpanzee became the focal animal, etc. (3) If the only chimpanzees in the Observation Areas had been observed at least twice, then a new focal animal was waited upon. If, after data collection began, the focal animal left the Observation Area, a second focal animal was followed. If the first focal animal returned to the Observation Area within 30 seconds of their departure, data collection resumed for that animal and any data collected for the second animal was omitted.

The Baseline condition differed slightly from the other two conditions with up to two 10-minute observations per chimpanzee for each day of observation (one AM and one PM). The Husbandry Training and Research Pod Activities conditions were task specific whereas the Baseline condition could have captured the chimpanzees engaging in a variety of activities, so observations were longer in duration to allow for a wider range of activity levels and allow for more accurate Baseline level of SDBs.

To best match the conditions of the Husbandry Training and Research Pod conditions, observations were only conducted while the focal animal was awake at the start of the observation.

During video coding sessions, focal animals were observed for a total of three minutes of qualifying footage. Qualifying footage included chimpanzees who were in view of the camera from the waist up; if the body parts involved in SDBs (hands, arms, or face) were not in view, the observer must have felt reasonably confident that SDBs were not taking place. Examples include: (1) Chimpanzee was standing quadrupedally with back to camera, front arms cannot be seen, but due to positioning of body, observer believed the chimpanzee was holding his weight with his front hands and could not exhibit SDBs with them. (2) Chimpanzee was sitting at the test window with one arm out of view, but shoulder could be seen to identify subtle movements. Movements only involving finger tips (indicating very gentle scratches) might have been missed, however, this represented only a small percentage of scratches (2.6%) coded from within all qualifying footage. If the chimpanzee was out of view (i.e. could not be seen as defined above) for more than three seconds, the observation continued with the next period of qualifying video footage. If another chimpanzee blocked the view of the focal animal for up to two seconds, the observation continued. Longer out of sight periods within the Qualifying Footage occurred on four occasions (see Appendix E1). When a chimpanzee did not reach a full three minutes of observation time within any given phase, their data were omitted from the relevant analyses.

Observation periods within all sessions were limited to a 30-second duration when at least six observations were available. Real-time data from Husbandry Training and Research Pod Activities were collected for the length of time the focal animals was in view and retroactively limited to 30-second time blocks using Observer software. However, if there were not enough observations from the real-time sessions to provide six 30-second periods for each chimpanzee, but at least three minutes were available overall, the full three-minute time period was distributed equally across the available observations (see Appendix C1).

Data on the chimpanzees' interest in research sessions were collected during the Self Recognition and Touchscreen Tasks phases. Instantaneous time sampling (Martin & Bateson, 2007) with one-minute scans was used to record the location of all chimpanzees within the Research Pod area (see Table 4.4)

where they could observe others or engage in the activities themselves. Estimated percentage of time spent in each location of the Research Pods was calculated to determine overall interest in research.

Table 4.4. Definitions of locations with the Research Pods for interest in research data, recorded in real time.

Locations	Definition
Tunnel	The tunnel entrance to the Research Pods where the chimpanzee could view the research activities.
Research Pod	The adjoining Research Pod rooms to the one with the primary test window used for research activities described in chapters 3 and 4. Activities at the test window could be viewed through the mesh divider or open door.
Test window area	The Research Pod room with the primary test window used for this research project. This window was adjacent to the public viewing windows (see Figure 2.4C).
At test window	Directly in front of the primary test window so that participation with test apparatus is possible. Positioning was noted regardless of participation. (Note: Data for this category were only recorded during the Touchscreen Tasks to monitor use.)

Data on disruptions, consisting of the chimpanzees' displays and fights, were recorded *ad libitum*, by the keepers in their daily report. For a display or fight to be included in the report, it had to be substantial enough (i.e. loud) to be heard from all areas of Budongo Trail, therefore it is likely that displays or fights that were subtle in nature were not represented in the data. Since each phase varied in length, the disruption data were calculated as a percentage of days within each phase that had at least one noteworthy disruption.

4.3.5 DATA ANALYSIS

4.3.5.1 EVENT BEHAVIOURS

Rates per minute were calculated by dividing event frequency, the number of point samples, by the duration of the observation sessions (during which the focal animals were always in view). Rates per minute were used to allow for comparisons across all conditions and phases, with each individual contributing one mean rate per condition/phase to avoid pseudo-replication of data (Dawkins, 2007).

4.3.5.2 INTER-OBSERVER RELIABILITY

Three-minute samples of qualifying footage across the Self Recognition and Touchscreen Tasks phases were compared to assess inter- and intra-observer reliability (IOR) for SDBs and vigilance behaviour. Samples were selected to ensure that each of these behaviours was represented at least five times. Behaviours that reached a high level of agreement with a Pearson correlation between and across observers were included in the analyses (Martin & Bateson, 2007).

Inter-observer reliability was tested by comparing data from six video samples with a naïve coder (AM): scratch ($r = 0.994, n = 5$), rub ($r = 0.721, n = 5$), vigilance/look ($r = 0.795, n = 6$). Intra-observer reliability was tested by comparing data from two sets of nine video samples, coded at least 48 hours apart, against each other: scratch ($r = 0.995, n = 6$), rub ($r = 0.993, n = 8$), vigilance/look ($r = 0.988, n = 9$). The categories for yawn³ and self groom did not occur frequently enough to be analysed for IOR, therefore from this point forward in this chapter, the term SDBs refer to scratching and rubbing. To ensure collapsing scratching and rubbing into one category did not mask any significant patterns (or lack thereof), independent analyses of scratch and rub were performed for all appropriate analyses. All results are reported in Appendix E2 with a separate mention in the results section if analyses differed from the collapsed data.

Inter-observer reliability was also calculated for dominance rankings across four raters. Each keeper's ratings were compared to the researcher's ratings with a high level of reliability: keeper 1 – CG ($r = 0.96, n = 11$), keeper 2 – SR ($r = 0.87, n = 11$), keeper 3 – SG ($r = 0.99, n = 11$).

4.3.5.3 STATISTICAL ASSUMPTIONS

To ensure that the statistics for the category of SDBs were not hiding differences for its behavioural components, scratch and rub, additional statistics were performed for all associated analyses (see

³ In a note on yawning, despite the lack of yawning during Husbandry Training and Research Activities where it only occurred once, the Baseline condition (where no training or testing occurred) included several instances of yawning across individuals.

Appendix E2). Descriptive statistics without statistical tests (due to sample size) were used in the analysis of the individual case study, for interest in research data, and for the comparison of individuals in support of group analyses.

4.4 RESULTS

4.4.1 ANALYSIS 1: ADDITION OF A COGNITIVE RESEARCH PROGRAMME

Data from six chimpanzees across all phases and conditions revealed that (a) SDBs were significantly different across the Baseline (median = 0.51), Husbandry Training (median = 1.11), and Research Pod (median = 1.33) conditions (Friedman's two-way ANOVA, $\chi^2(2) = 9.0, p = .011, n = 6$, see Figure 4.10). Wilcoxon tests were used to follow up this finding, where the alpha criterion was reduced to 0.0167 to correct for multiple tests. SDBs did not differ between Baseline and Husbandry Training ($T = 21, r = 0.9, p = 0.03, n = 6$), nor did Baseline differ from the Research Activities ($T = 21, r = 0.9, p = 0.03, n = 6$). Husbandry Training did not significantly differ to the Research Activities ($T = 12, r = 0.21, p = 0.60, n = 6$). We can conclude that while there appears to be a difference between the three conditions, with baseline levels lower than both husbandry and training, pair-wise comparisons were not significant.

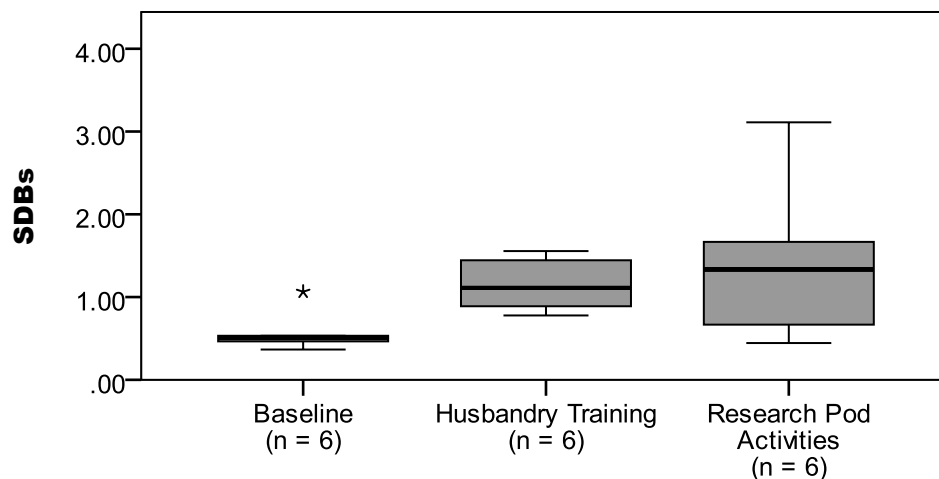


Figure 4.10. A comparison of the median and interquartile range (IQR) of SDBs rate per minute across the three conditions: Husbandry Training, Research Pod Activities, and Baseline. Whiskers represent 5th and 95th percentiles; circles show outliers with numbers to represent outlier data points. Outlier in the Baseline condition represents Cindy (1.06), the highest exhibitor of SDBs overall (see Appendix E3).

To get a broader picture of the group's performance, we examined the conditions during the first phase of research, Initial Training, where more individuals participated ($n = 9$; data from two chimpanzees

were omitted due to a lack of interest in Husbandry Training). SDBs significantly differed across conditions (Friedman's two-way ANOVA, $\chi^2(2) = 6.35, p = 0.04$, see Figure 4.11): Baseline (median = 0.6), Husbandry Training (median = 1.67), and Research Activities (median = 0.67). Follow-up Wilcoxon tests showed that compared to Baseline, SDBs were significantly higher during Husbandry Training ($T = 44, r = 0.85, p = 0.01, n = 9$), but were not significantly different during Research Activities ($T = 26, r = 0.14, p = 0.68, n = 9$) and Husbandry Training did not significantly differ from the Research Pod condition ($T = 6, r = -0.45, p = 0.18, n = 9$). Additional calculations examining scratch and rub as separate data sets showed a significant difference for the scratching data only, suggesting that the collapsed category of SDBs was only significant due to scratching rates (see Appendix E2). We can conclude that the difference across all conditions is due to the Husbandry Training condition being higher than the Baseline condition.

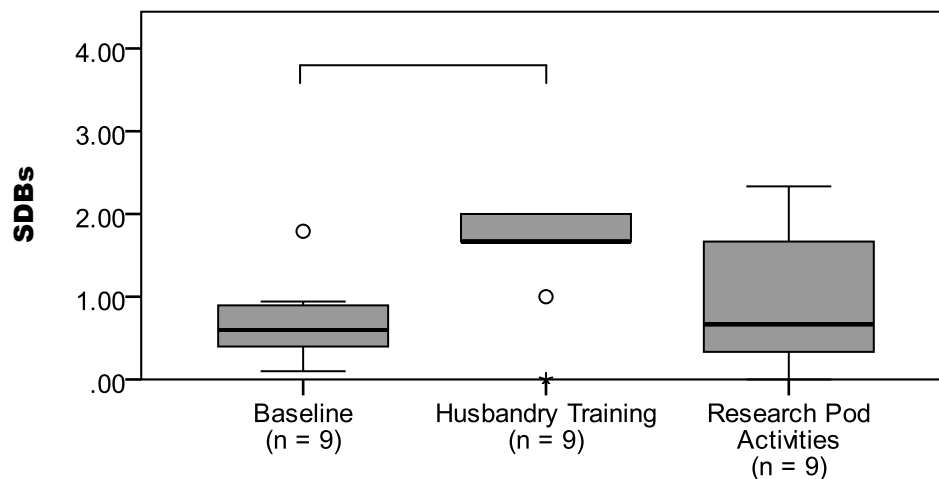


Figure 4.11. A comparison of the median and interquartile range (IQR) of SDBs rate per minute across all conditions during the Initial Training phase: Baseline, Husbandry Training, and Research Pod Activities. Whiskers represent 5th and 95th percentiles, circles show outliers. Outlier in the Baseline condition represents Cindy (1.79), the highest exhibitor of SDBs overall (see Appendix E3) and outliers in the Husbandry Training condition represent Ricky (1.00) and Kindia (0.00). Note that a comparison of all 11 chimpanzees was not possible due to a lack of participation from two chimpanzees during the Husbandry Training condition.

Data from six chimpanzees across all phases revealed that, (b) rates of SDBs (transformed, log+1) did not significantly differ across phases (RM ANOVA, $F(2, 10) = 2.68, p = 0.12, n = 6$, see Figure 4.12): Initial Training (mean = 0.55, SE mean = 0.14), Self Recognition (mean = 0.86, SE mean = 0.25), and Touchscreen Task phases (mean = 0.94, SE mean = 0.13). We can conclude that the phase of research did not impact SDBs.

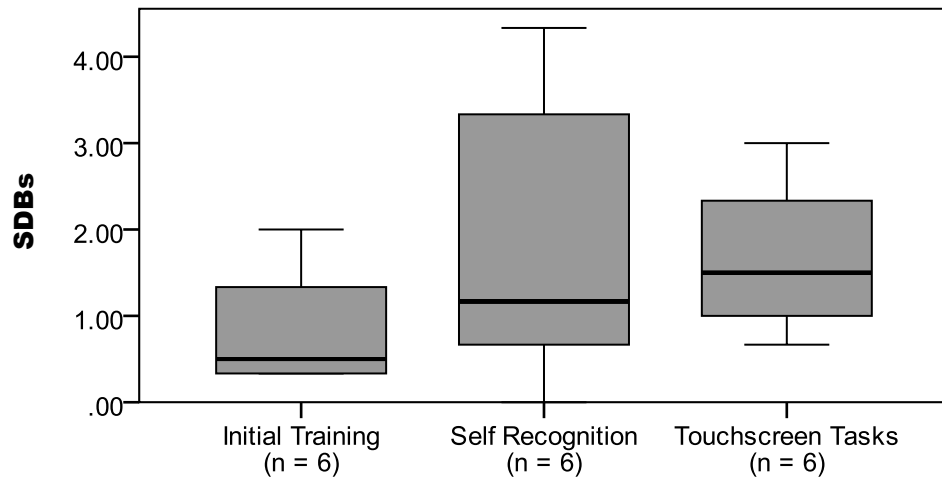


Figure 4.12. A comparison of the median and IQR of SDBs rate per minute across the three phases within the Research Pod Activities: Initial Training, Self Recognition, and Touchscreen Tasks. Whiskers represent 5th and 95th percentiles.

4.4.2 ANALYSIS 2: GROUP TRAINING AND TESTING

Data from six chimpanzees across all phases revealed that, (a) SDBs (transformed, log+1) did not significantly differ based on social context (T-test, $t(5) = -1.24$, $p = 0.27$, $r = 0.48$, $n = 6$, see Figure 4.13): alone (mean = 0.76, SE mean = 0.19) and near others (mean = 0.94, SE mean = 0.25). Additionally, (b) vigilance rates did not significantly differ based on social context (T-test, $t(5) = 1.2$, $p = 0.29$, $r = 0.47$, $n = 6$, see Figure 4.14): alone (mean = 6.49, SE mean = 1.45) and near others (mean = 4.5, SE = 1.03). We can conclude that social context did not impact SDBs or vigilance levels.

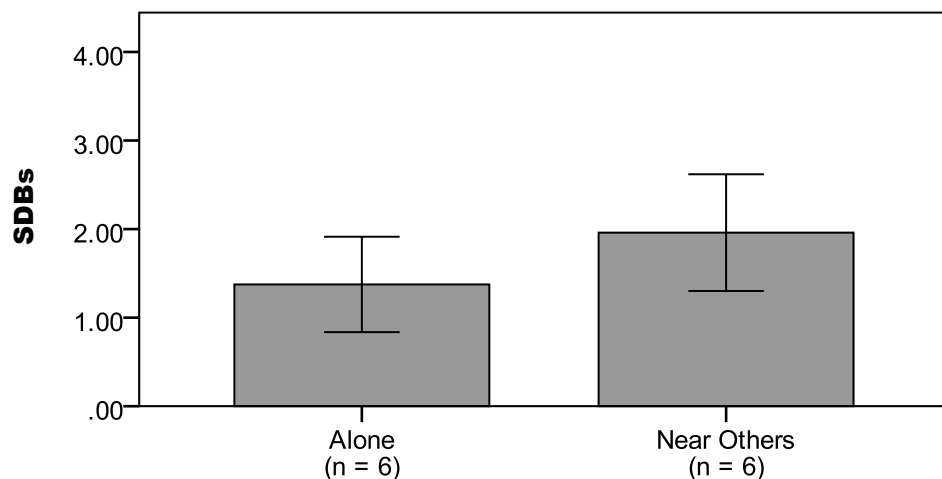


Figure 4.13. A comparison of the mean (+/- 1 SE) SDBs rate per minute when chimpanzees were alone and near others (i.e. within one arms-length of the focal animal). Data are from both the Self Recognition and Touchscreen Task phases.

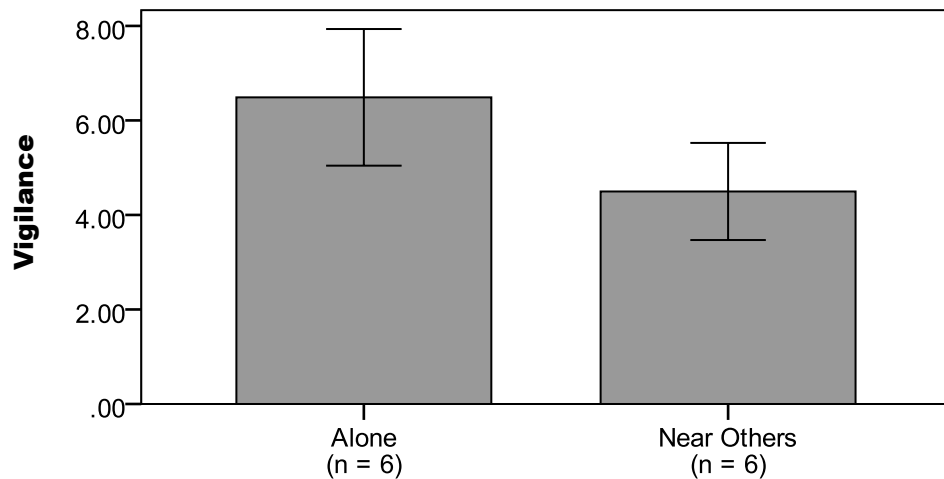


Figure 4.14. A comparison of the mean (\pm 1 SE) vigilance rates per minute when chimpanzees were alone and near others (i.e. within one arms-length of the focal animal). Data are from both the Self Recognition and Touchscreen Task phases.

4.4.3 ANALYSIS 3: CASE STUDY (GROUP VS INDIVIDUAL)

One chimpanzee was particularly well motivated to participate and, in addition to regular group sessions, could be tested individually. We compared her data when participating in individual training (i.e. she was voluntarily closed into the Research Pods and while she could leave at any time, no one could enter) versus group training (i.e. all chimpanzees could enter and exit at any time during the session). Cindy had previous experience with being closed into the Research Pods by herself. She regularly volunteered to be closed into the Bed Area when others would opt to go outside in the morning while keepers would clean the enclosures. During this time she could hear the others, but they could not enter. Two sessions each from individual and group training sessions, matched for similar content, were compared. The data show a small decrease in Cindy's rates of (a) SDBs and (b) vigilance during individual research sessions (SDBs: mean = 3.4; vigilance: mean = 3.45) versus group research sessions (SDBs: mean = 4.14; vigilance: mean = 4.44) suggesting that she found these testing experiences to be similar (see Figures 4.15 and 4.16)

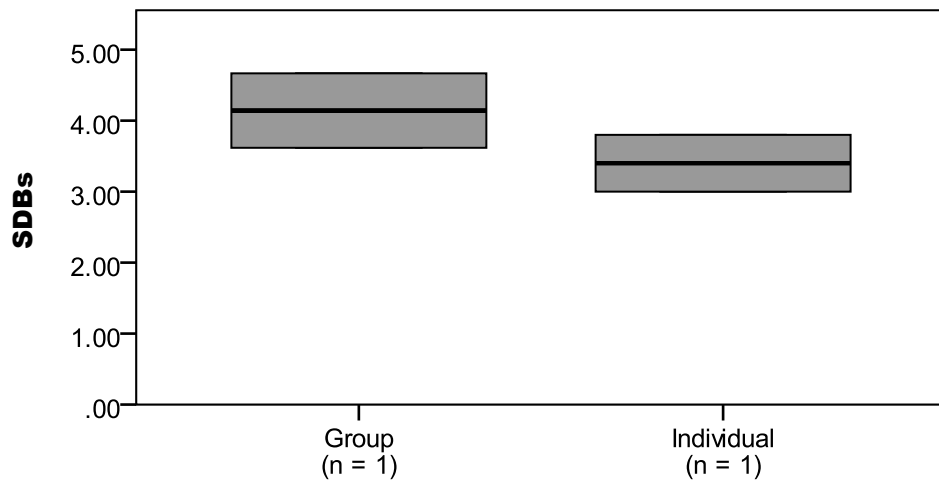


Figure 4.15. A comparison of the median and IQR of SDBs rate per minute exhibited by Cindy during group and individual training (2 sessions each). Whiskers represent 5th and 95th percentiles.

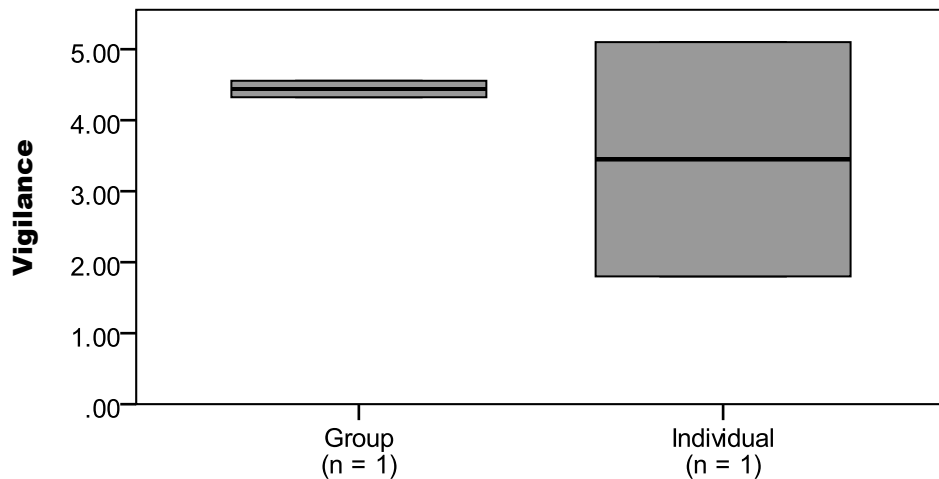


Figure 4.16. A comparison of the median and IQR of vigilance rates per minute exhibited by Cindy during group and individual training. Whiskers represent 5th and 95th percentiles.

4.4.4 ANALYSIS 4: VIGILANCE

Data from six chimpanzees who participated in both the Self Recognition and Touchscreen Task phases revealed that vigilance was not significantly correlated with group rank (Spearman's correlation coefficient, $r = -0.09$, $p = 0.87$, $n = 6$, see Figure 4.17). If the rate for the highest exhibitor of SDBs (Cindy, rank 11) was omitted as an outlier, vigilance became significantly correlated with group rank (Spearman's correlation coefficient, $r = -0.8$, $p = 0.05$, $n = 5$), where rates of vigilance increased as rank increased (as represented by lower numbers).

Although removal of the outlier (Cindy) resulted in a significant correlation, when examining data from the Self Recognition phase alone, where more individuals could be included in analyses, vigilance was not significantly correlated with rank within the group (Spearman's correlation coefficient, $r = 0.07$, $p = 0.87$, $n = 8$, see Figure 4.18). The distribution appears to be quadratic, but this regression was also not significant ($r^2 = 0.648$, $df = 7$, $p = 0.07$). If Cindy (rank 11) is omitted from the data set, vigilance was still not significantly correlated with group rank (Spearman's correlation coefficient, $r = -0.29$, $p = 0.36$, $n = 7$). We can therefore conclude that there is no significant relationship between rank and vigilance levels.

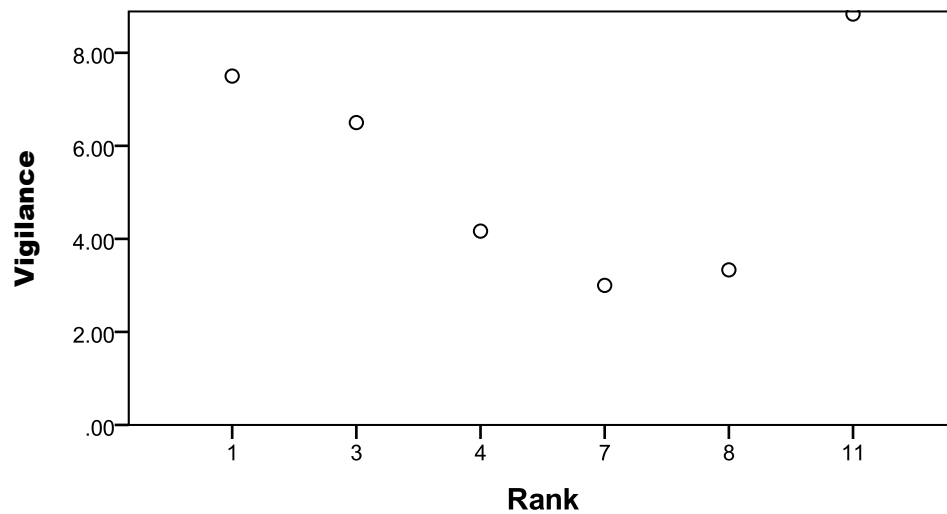


Figure 4.17. A comparison of chimpanzee rank (see Appendix A) versus the rate per minute of vigilance for individuals participating in both the Self Recognition and Touchscreen Task phases ($n = 6$). Rank 1 – 11 represents highest to lowest, respectively.

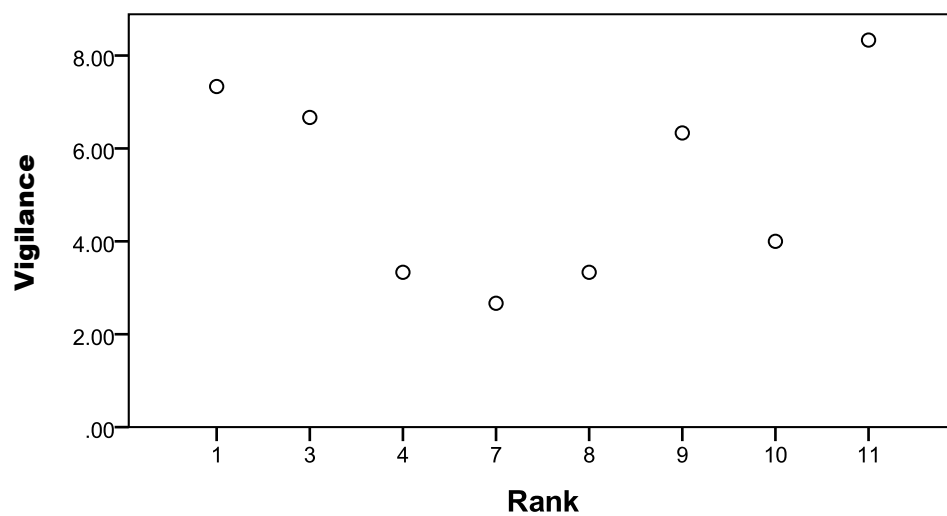


Figure 4.18. A comparison of chimpanzee rank (see Appendix A) versus the rate per minute of vigilance for individuals participating during the Self Recognition phase ($n = 8$). Rank 1 – 11 represents highest to lowest, respectively.

4.4.5 ANALYSIS 5: REWARD CONTINGENCY

During training and testing, it became apparent that additional factors might have played a role in the performance of SDBs. An assessment on two methodological variations within the Research Pod Activity phases of the video taped Research Pod sessions (Self Recognition and Touchscreen Task phases) was performed in post hoc analyses: reward contingency (this section) and visual access to keepers (see Section 4.4.6)

Rewards were contingent upon the chimpanzees' actions during sessions with keeper-led PRT activities (timing and amount of rewards obtained were based on performing a correct task) but were not contingent upon the chimpanzees' actions during sessions without an interactive task (where food rewards were offered on a variable schedule regardless of participation). Data from six chimpanzees who participated in all phases revealed that SDBs (transformed, $\log+1$) did not significantly differ based on reward contingency (T-test, $t(5) = 0.49$, $p = 0.65$, $r = 0.21$, $n = 6$, see Figure 4.19): sessions in which rewards were contingent upon actions (Initial Training and Touchscreen Tasks; mean = 0.77, SE mean = 0.13) and sessions in which rewards were not contingent upon actions (Self Recognition; mean = 0.86, SE mean = 0.25). We can conclude reward contingency did not impact SDBs.

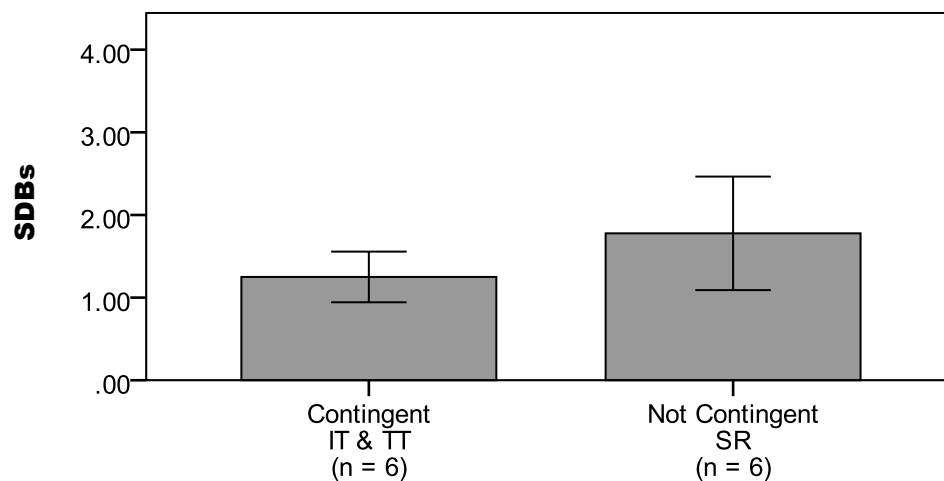


Figure 4.19. A comparison of the mean (± 1 SE) SDBs rate per minute for conditions in which rewards were contingent upon the chimpanzee's actions, Initial Training (IT) and Touchscreen Tasks (TS) and were not contingent upon the chimpanzees' actions, Self Recognition (SR).

4.4.6 ANALYSIS 6: VISUAL ACCESS TO KEEPERS

When the training and testing equipment used for the Self Recognition and Touchscreen Task phases was not in place, specifically the mirror and touchscreen monitor (see Figures 4.5 – 4.9), the chimpanzees had visual access to their keepers through the test window during Research Pod sessions. Data from six chimpanzees who participated in all phases revealed that in accordance with the hypothesis, SDBs were significantly different in relation to visual access to keepers (T-test, $t(5) = -2.67$, $p = 0.04$, $r = 0.77$, see Figure 4.20): visual access to keepers (Initial Training: mean = 0.83, SE mean = 0.28) and no visual access (combined rate for Self Recognition and Touchscreen Tasks: mean = 1.72, SE mean = 0.48). We can conclude that removing visual access to keepers impacted SDBs.

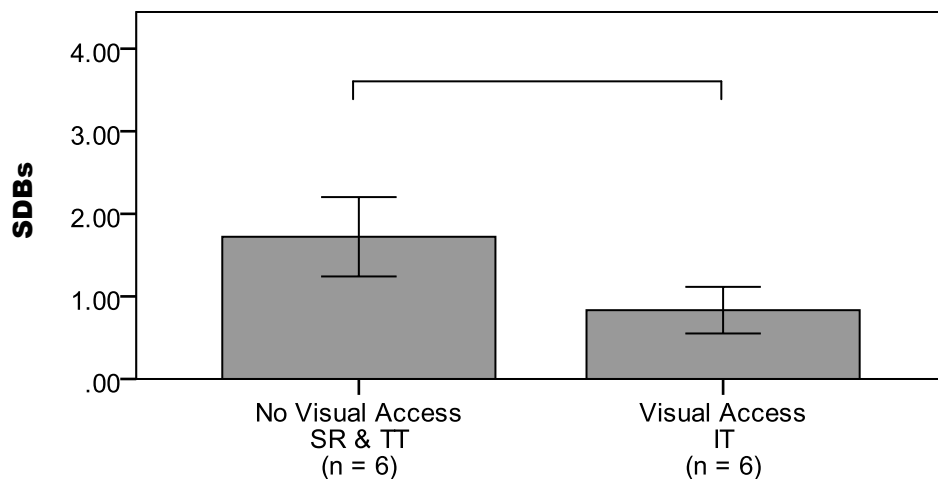


Figure 4.20. A comparison of the mean (± 1 SE) SDBs rate per minute for conditions in which chimpanzees had visual access to their keepers (IT = Initial Training) and did not have visual access to their keepers (SR = Self Recognition; TT = Touchscreen Tasks). The adjoining bracket highlights significance.

4.4.7 ANALYSIS 7: INTEREST IN RESEARCH

It was hypothesised that (a) those who participated the most overall, would have the lowest levels of SDBs in the Research Pods. (a) SDBs were not significantly correlated to overall interest in the research sessions during the Initial Training phase when the entire group could be compared (Spearman's correlation coefficient, $r = -0.26$, $p = 0.44$, $n = 11$, see Figure 4.21). To ensure the result was not simply assessing the impact of project initiation, an examination of the SDBs from those who participated in all phases of research was also conducted. There was no correlation between rank and SDBs across the

course of the project (Spearman's correlation coefficient, $r = -0.03$, $p = 0.95$, $n = 6$). We can therefore conclude that there is no relationship between interest in the research sessions and SDBs.

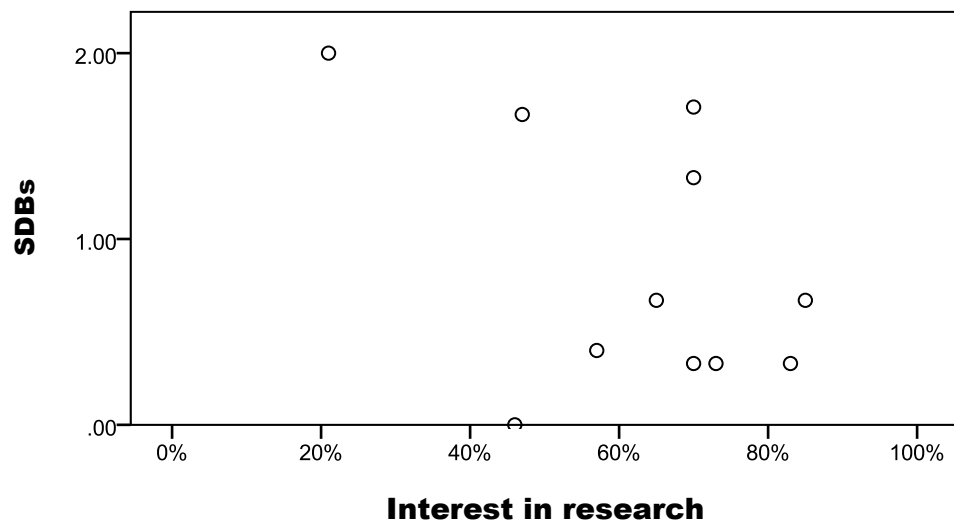


Figure 4.21. A comparison of the percentage of interest in the research sessions versus the rate per minute of SDBs during the Initial Training phase ($n = 11$). Circles represent data points for each chimpanzee.

In accordance with the hypothesis, (b) females were significantly more interested in the research sessions than males (T-test, $t(9) = -2.99$, $p = 0.02$, $r = 0.71$, $n = 11$, see Figure 4.22): males (mean = 51%, SE mean = 7.151) and females (mean = 76.2%, SE mean = 3.25). When interest in the research sessions was considered in terms of location and proximity to the primary test window (where the touchscreen was located), there were no sex differences when the chimpanzees were in the tunnel, in the Research Pods, or directly in front of the test window (see Table 4.6 and Figure 4.23). We can conclude that although females were more interested in the research sessions than males overall (i.e. coming in to pods for a research session), once the chimpanzees were in the research area, there was no sex difference between time spent in each location (proximity to primary test window).

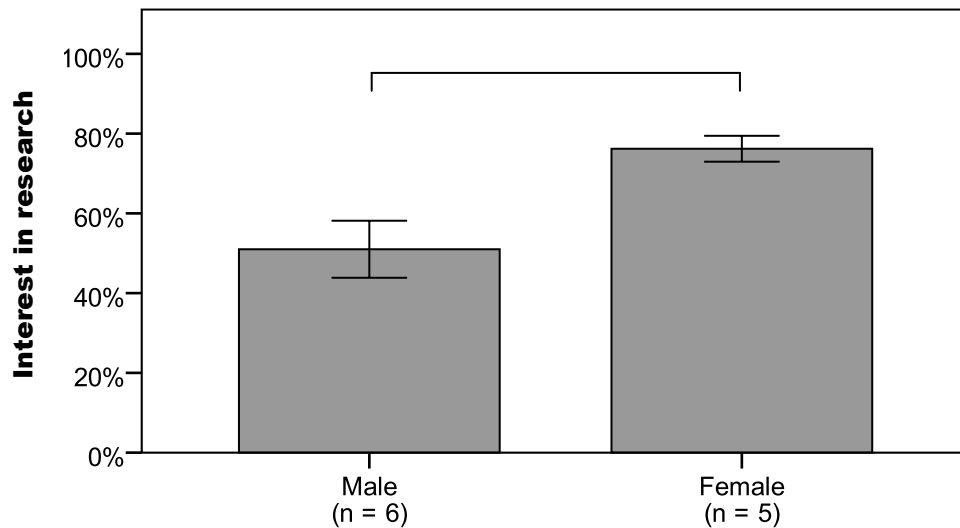


Figure 4.22. A comparison of the mean (\pm 1 SE) percentage of interest in the research sessions across all phases of research by sex.

Table 4.6. Statistical results for Spearman correlation coefficients between sex and interest in research data showing breakdown of locations in which the chimpanzees were present.

Location	Males (mean %; SE)	Females (mean % ; SE)	Test statistic (t)	df	p	Effect size (r)
Tunnel	23.67; 7.85	11.20; 4.88	1.28	9	0.23	0.39
Research Pods	53.57; 5.43	56.40; 7.20	-0.31	9	0.76	0.10
Test Window	23.00; 7.33	32.80; 9.18	-0.85	9	0.42	0.27

Note: The location of Research Pods does not include when participants were in front of the test window.

(c) Rank was not significantly correlated with interest in the research sessions (Spearman's correlation coefficient, $r = 0.28$, $p = 0.41$, $n = 11$, see Figure 4.23). When broken down into where the chimpanzees were located once they were a part of a session (see Figure 4.24), there were no rank differences when the chimpanzees were in the tunnel (Spearman's correlation coefficient, $r = 0.00$, $p = 1.00$, $n = 11$), in the Research Pods (Spearman's correlation coefficient, $r = -0.05$, $p = 0.89$, $n = 11$), or directly in front of the test window (Spearman's correlation coefficient, $r = 0.03$, $p = 0.93$, $n = 11$). We can conclude that there is no relationship between rank and interest in research sessions, regardless of location within the Research Pods.

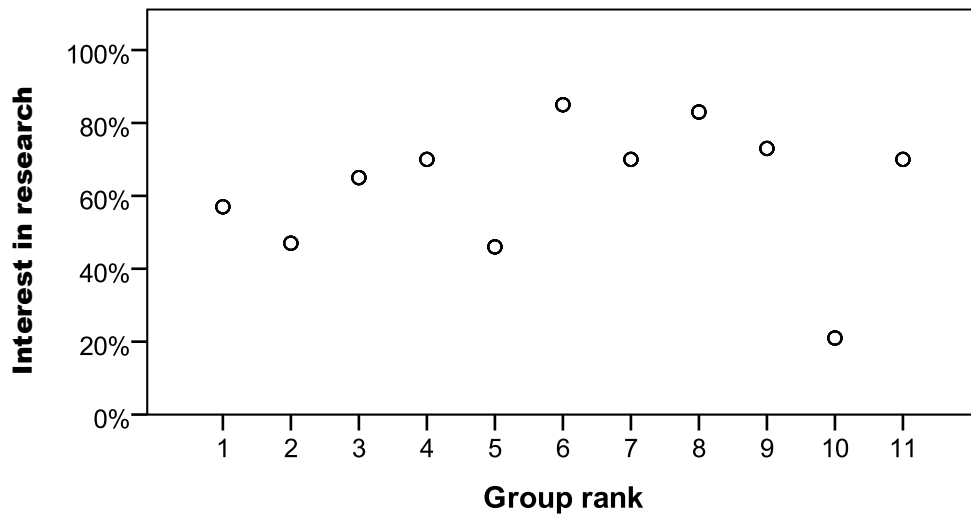


Figure 4.23. A comparison of chimpanzee rank (see Table 4.2) versus the percentage of overall interest in research sessions throughout all phases of research (n = 11). Rank 1 – 11 represents highest to lowest, respectively.

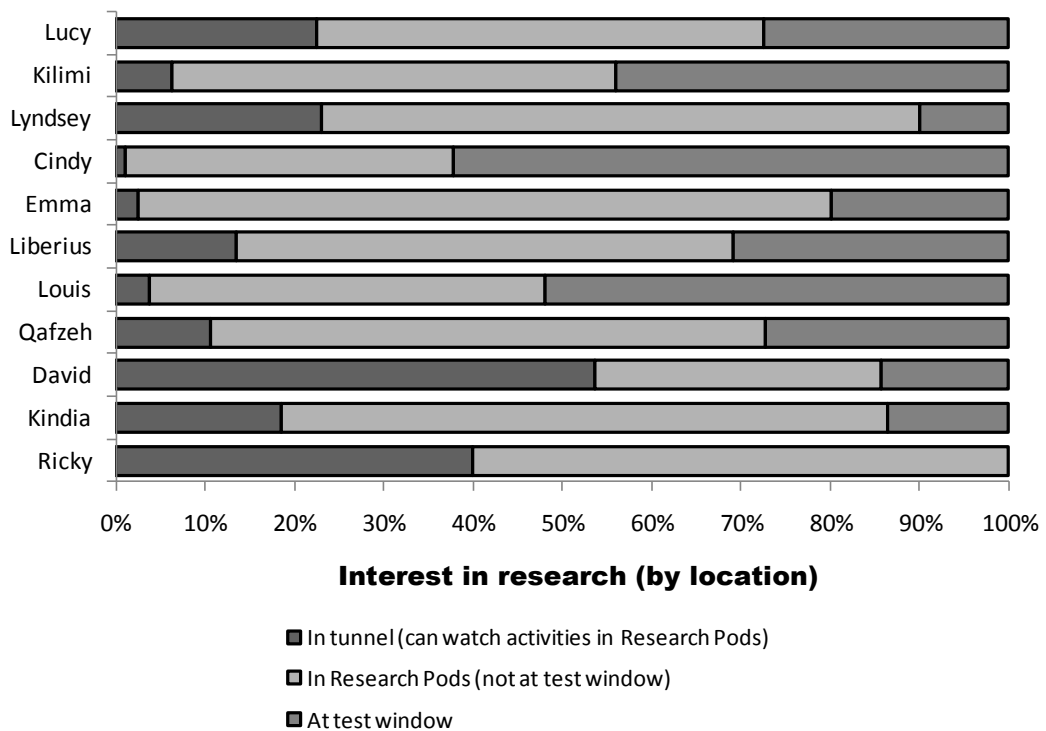


Figure 4.24. Percentage of interest in research sessions for each chimpanzee (separated by location within the Research Pods). Chimpanzees are ordered from the top down from the highest rate of overall interest (Lucy) to the lowest rate (Ricky).

In terms of social context and the ongoing dominance battle (see Section 2.2), (d) there was no obvious relationship between the percentage of days with disruptions recorded by keepers and interest in research sessions or SDBs (see Table 4.7 and Figure 4.25). Although lower disruptions were associated

with higher interest in the research sessions during the Self Recognition phase, it was not a strong pattern throughout the course of the study. Vigilance appeared to fall in line with the disruption pattern between Self Recognition and Touchscreen Tasks (see Table 4.7 and Figure 4.25), however without data for the Initial Training phase, it is difficult to assess.

Table 4.7. Mean scores for disruptions, interest in research, SDBs, and vigilance across the three phases of research.

Phase	Disruptions (% of days)	Interest in research (%)	SDBs (rate/min)	Vigilance (rate/min)
Initial Training	17.60	69.77	0.55	--
Self Recognition	14.29	75.00	0.86	5.17
Touchscreen Tasks	16.67	58.33	0.94	5.67

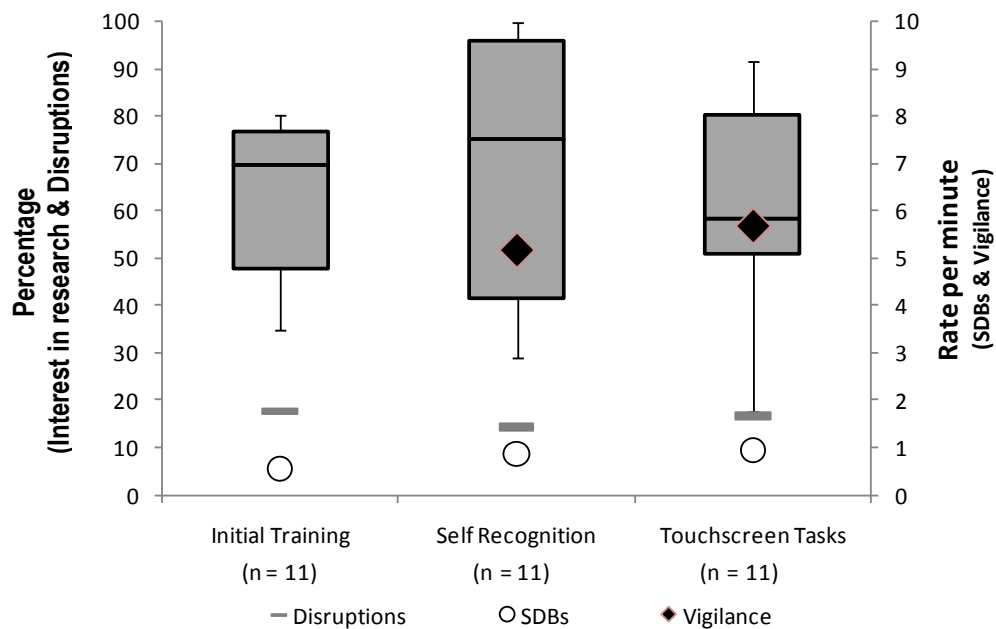


Figure 4.25. A comparison of the median and IQR of the percentage of interest in research (whether or not a chimpanzee entered the Research Pods during a research session) across all phases of research, as shown by the boxplots, in relation to the percentage of days within a phase that had disruptions from the group (i.e. displays and fights; grey dashes) and the mean rates of SDBs (circles) and vigilance (black diamonds). Whiskers represent 5th and 95th percentiles; vigilance omitted during Initial Training as live coding only.

4.4.8 SUMMARY OF RESULTS

Our analyses indicate that there was a significant difference between the Baseline, Husbandry Training, and Research Activities conditions for the six chimpanzees who were present during each phase of the research project; however, further analyses did not reveal any significant differences between

conditions. An analysis of the three conditions during the Initial Training period revealed a difference between the conditions, due to the Husbandry Training differing from the Baseline condition. In an in-depth look at potential differences within the Research Pod condition, comparing all the phases of cognitive research, no significant differences are present. Group testing did not appear to be an issue for this group in terms of SDBs nor vigilance behaviours and in a case study of an individual who was comfortable participating in research sessions by herself and when others were present, there was a negligible difference in her rate of SDBs and vigilance behaviours suggesting that she finds the group versus individual testing experiences to be similar. Overall these findings suggest that the addition of a cognitive research programme did not negatively impact the welfare of the group. When analysing two methodological changes as a result of the types of research offered, while there was no significant relationship between SDBs and reward contingency, SDBs were significantly lower during tasks in which chimpanzees had visual access to keepers. Analyses on rank suggest that this did not impact on vigilance overall; although there was a significant correlation after an outlier was removed (when looking at both Self Recognition and Touchscreen Task phases), an analysis of the Self Recognition phase alone (with more participants), negated that finding. Interest in research was examined in several ways and while there was a relationship between sex and overall interest in research (with females being more interested in research sessions than males), there were no significant differences in preferred location within the Research Pods (i.e. how far into the Research Pods they are willing to go). Further analyses on interest in research sessions suggest that interest had no relationship with rank, performance of SDBs, and disruptions from the group.

4.5 DISCUSSION

The addition of a cognitive research programme was a major event for the chimpanzee group in Budongo Trail. For a group that was naïve to cognitive research and relatively new to positive reinforcement training, the full-time presence of a researcher offering research sessions and observing them on- and off-exhibit may have had a considerable impact upon behaviour. As the welfare of the animals is of the utmost importance, the primary goal of this study was to assess the welfare of the chimpanzees during the development of the research programme.

4.5.1 ADDITION OF A COGNITIVE RESEARCH PROGRAMME

The addition of a cognitive research programme was examined in several analyses. The limited difference between the conditions suggests that participating in the research (either actively or through observation from within the Research Pods) was not any more stressful for the chimpanzees than participating in their regular activities around their enclosure. To elaborate further, when the initial phase of the research project was examined across conditions (with data for only 9 individuals due to lack of participation during Husbandry Training), a clear difference was found between the Baseline condition and the Husbandry Training condition, mainly due to increased scratching. There was considerable individual variation in all measures: interest in research, SDBs, and vigilance. Regardless, it is clear that the Baseline condition was similar to the Research Pod condition, suggesting that the addition of an on-exhibit cognitive research programme did not cause anxiety.

Further exploration of SDBs in the three different phases of research (i.e. Initial Training, Self Recognition, and Touchscreen Tasks) found no difference across phases. Since Initial Training was based on training behaviours that the chimpanzees had previous, yet limited, experience with (e.g. targeting to an object), it was expected that the subsequent phases would have higher rates of SDBs than Initial Training. With Initial Training expected to have the lowest rates, Touchscreen Tasks were expected to have the highest rates, but there was no statistical difference; SDBs did not reflect the challenge of performing a task, contradicting previous research where SDBs increased in relation to an increase in task novelty or difficulty (Itakura, 1993; Leavens et al., 2001). However, perhaps the level of difficulty in previous research tasks played a role, as the beginning stages of this cognitive research programme included new activities that were not very cognitively demanding.

4.5.2 GROUP TRAINING AND TESTING

Contrary to previous research in which chimpanzees exhibited more SDBs in crowded compared to less crowded enclosures (Aureli & de Waal, 1997), an examination of the social context of the research sessions suggested that group access did not impact SDBs. However, Aureli and de Waal were reporting on housing conditions rather than within a group testing research context, so this is clearly not a perfect

comparison. Nonetheless, given that in the current study, participation was voluntary and the chimpanzees could leave at any time, the social context was similar: crowded versus less crowded, and near others versus alone.

One possible explanation of the finding is related to study design; having choice and control over their own participation in the research might have been sufficient in maintaining SDB rates at Baseline levels, suggesting that training and testing in a group environment is not more stressful than when the chimpanzees choose to participate in other activities. Furthermore, the case study for Cindy's individual training versus group training showed a negligible difference in SDBs, a likely product of her previous experiences and willingness to be separated from the group for periods of time (a characteristic not shared by the rest of the group but one which could well emerge with further training and experience). Overall, the lack of a statistical difference in rates of SDBs is particularly important. Despite higher rates in comparison to previous studies in the field and in captivity (see Table 4.1), the consistency across conditions suggests SDBs were not compromised by the addition of the research programme.

4.5.3 VIGILANCE

This study is the first to assess vigilance in a cognitive setting as previous research on vigilance focused on predatory situations or wild group contexts (Treves, 2000; Kutsukake, 2003b & 2007). Despite the variation in findings on the role of vigilance (Chance, 1967; Pulliam, 1973; Treves, 2000; Kutsukake, 2003b & 2007), it was hypothesised (in accordance with anecdotal data from a similar research setting: Leighty et al., 2011) that higher ranking individuals would exhibit more vigilance behaviours than lower ranking individuals. However, there was no effect of rank on rate of vigilance behaviours. Moreover, vigilance behaviours did not differ according to social context (alone versus near others). Given the nature of the enclosure space, one might assume that the chimpanzees would be more vigilant when they were alone but others could enter, compared to when others were already in the Research Pods with them because as the group size increases, vigilance becomes a shared duty and individual rates decrease (Pulliam, 1973). However, it was suggested that vigilance would increase when others were in proximity as vigilance behaviour is directed to a known threat or competitor, such as a group member within view (e.g. Kutsukake, 2003b & 2007), in addition to an unknown threat, such as a predator (or in

our situation, the chimpanzee that might yet choose to enter the area). Vigilance behaviour was consistent throughout in this study suggesting that this group was equally vigilant regardless of the circumstance.

Since vigilance did not differ in relation to rank or to group context, perhaps the chimpanzees are monitoring other things within their environment, such as keeper activity in order to monitor when exits will be closed. Or given the dominance struggle within the group (see Section 2.2), maybe the individuals chose to be equally vigilant regardless of the situation because as much as they are part of a group, chimpanzee politics often result in dynamic relationships (de Waal, 1982).

4.5.4 REWARD CONTINGENCY AND VISUAL ACCESS

Further analyses of methodological differences in each phase of research (i.e. reward contingency and visual access to keepers) found no statistically significant difference in rates of SDBs in relation to whether or not rewards were contingent upon the chimpanzees' actions during the research sessions. However, SDBs were found to be lower when keepers were visible during training and testing (although this pattern was not significant for either scratch or rub when considered independently). Collapsing scratch and rub into a single category proved to be acceptable for this study as the separate results, with a few exceptions, were generally equivalent.

The difference in rates of SDBs across conditions could be related to their previous experiences, where keepers were always visible; the only training the group was a part of prior to the onset of this study involved face-to-face interaction with their keepers (C. Gresswell, personal communication, 2008). Given that both the husbandry training and research programme were new to the chimpanzees, they might habituate to the removal of visual access and over time their rates of SDBs might return to baseline levels. While it is important to provide new challenges for captive animals (Meehan & Mench, 2007), the seemingly simple adjustments in protocol that go along with the new challenges, may be more stressful to the chimpanzees than researchers might have anticipated (i.e. visibility of keeper during Research Pod condition). However, not all changes in the protocol impacted the rates of SDBs observed (i.e. reward contingency) suggesting that changes to research methodologies should be ongoing and assessed on an individual basis.

Testing chimpanzees on computerised tasks has worked well in several facilities and allowed an unprecedented insight into the chimpanzee mind (e.g. Beran et al., 1998; Kawai & Matsuzawa, 2000; Leavens et al., 2001; Shumaker et al., 2001; Ross et al., 2010). For example, the Primate Research Institute (Kyoto University, Japan), holds daily computerised tests within transparent research enclosures (Cohen, 2010). It is unclear whether visual access is most important during the initial stages of research development, or only for more research naïve groups. Additional research would help validate any relationships between these factors and welfare. With many zoo animals being new to cognitive research and some zoos taking on the task of constructing new research facilities, it could possibly benefit researchers and zoo management to incorporate visual access into their new research enclosure designs. Research areas with a larger focus on visual access for both chimpanzees and staff could be beneficial for all involved.

4.5.5 INTEREST IN RESEARCH

When looking at research from a welfare point of view, interest in research (determined by presence in the Research Pods during sessions) serves as a clear indicator of interest and allows an assessment of the potential implications the research has on welfare. We anticipated that the chimpanzees who were the most interested in the research sessions would have the lowest rates of SDBs, either because more experience with an activity leads to less uncertainty and lower rates of SDBs or because low levels of uncertainty and low SDBs can lead to more interest in an activity. However, there was no relationship between percentage of interest in research and SDBs. One possible explanation is that the activities offered were varied enough to keep their interest and to keep them guessing (i.e. uncertain) about what would happen next; a good thing for welfare based on the suggested value of problem solving opportunities (Meehan & Mench, 2007).

The sex difference in research interest fits with previous findings that female chimpanzees learn how to perform cognitive activities (i.e. termite fishing) earlier in development than males (Lonsdorf, 2005) and as adults, have been found to exhibit more of an interest in and are more efficient than males when it comes to tool use (frequency and duration of termite fishing: McGrew, 1979; accuracy in nut cracking: Boesch & Boesch, 1981, as cited in Lonsdorf, 2005). It is suggested that males are more likely to focus

more on learning about tasks that are important to their reproductive success, specifically in dealing with dominance relationships (Lonsdorf, 2005).

Social factors undoubtedly play an important role in the lives of chimpanzees (de Waal, 2007), regardless of the situation, be it research or everyday life. With a struggle for dominance occurring throughout the project, these chimpanzee politics often determined whether anyone came into the Research Pods at all. While a dominance struggle is arguably stressful for all chimpanzees in the group, assuming that the high-ranking chimpanzees would be more preoccupied by the struggle than the low-ranking chimpanzees, it is surprising to see that there was no difference in research interest based on rank.

Since the dominance struggle seemed so central to group life, it was thought that interest in research sessions would decrease as disruptions from the group (i.e. large-scale displays and fights) would increase, but we did not find this to be the case. Perhaps this, along with the similar research interest from high and low ranking individuals supports the idea that the research sessions were enriching and sometimes preferred over other activities, including serving as a potential escape from the dominance struggle. However, there are limitations to the *ad libitum* data collection methods, as smaller disruptions were likely to have been missed and fights were not recorded when they occurred at night, with the only indication being wounded (or tired-looking) chimpanzees in the morning.

The dominance struggle sometimes continued in the Research Pods, as a location to exhibit displays and make loud noises (as one wall was made of steel and the test windows were lined with Perspex; both excellent conductors of noise when hit or kicked) that subsequently scared off any active participants. While chimpanzees are certainly curious (Goodall, 1971), by choosing to be present for research sessions when so many other things are going on in their lives, they are making a big statement about their preferences. In addition to the struggle for dominance, these chimpanzees also live in a highly enriched environment with a great deal of choice and control throughout their day, from where they decide to hang out to whether or not they participate in the training or enrichment offered by the keepers.

4.5.6 SDBS AS A WELFARE INDICATOR

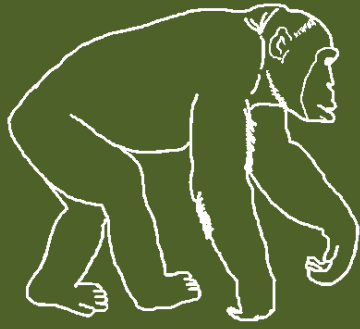
Despite relatively widespread use as a dependent measure, the interpretation of SDBs can be challenging. For example, inconsistencies in rates of performance occur across species and contexts (as reviewed by Maestriperi et al., 1992). Yawning has been listed as a SDB indicating uncertainty and anxiety among non-human primates in several studies (Hadidian, 1980; Baenninger, 1987; Schino et al., 1990; Castles et al., 1999; Troiso, 2002; Baker & Aureli, 1997); however, data within this chapter suggest that yawning might not be an indicator of uncertainty in the situations tested. While the behaviour was identified, it was omitted from analyses due to low frequency of occurrence. This is not to propose that yawning should be eliminated from the SDB terminology but more detailed reports on frequency of occurrence for different SDBs are needed to more fully assess their relative value. Reports seldom provide separate yawn data as it is usually collapsed into a general category of “abnormal” (Pomerantz & Terkel, 2009), “distress”, “anxiety-related” (e.g. Perdue et al., 2011), or displacement (Schino et al., 1990; Troisi, 2002) behaviours. Without consistent reporting methodology, it is difficult to ascertain the importance of the behaviour and posits the question of its usefulness in identifying uncertainty.

While collapsing scratch and rub into a single category was suitable for this study (with any differences specifically identified), with a variety of ways in which results are presented across the literature, it can be difficult to pull apart analyses that represent a combination of behaviours; which, in turn, adds to the difficulty in generalising a level of SDBs that should cause concern for welfare. Given the potential differences in motivational drives behind different SDBs (see Chapter 7), if researchers find it best to collapse behaviours into a single category, it would be helpful for the results to also include a brief breakdown of the scores for each behaviour.

4.6 SUMMARY AND CONCLUSIONS

As a whole, the data suggest that training chimpanzees for cognitive tests does not compromise welfare, but rather that the chimpanzees’ repeated interest in the challenges offered in research sessions implies that for some, the research activities are reinforcing. These results give us an idea of how this group of chimpanzees reacted to certain research-based situations, and can inform future study design, and possibly even improve both enclosures and research areas for the development of

similar cognitive research programmes within zoos in the future. Monitoring welfare should be integral to any zoo research to assess positive and negative indicators of welfare to help identify tasks that are enriching and mentally stimulating. Not only is it important ethically and for the quality of research, but also for the success of public engagement with science. With zoos providing their supporters with more opportunities to gain a better understanding of behaviour, cognition, and welfare, the importance of both wellbeing and conservation of primates can be promoted to a wider audience.



CHAPTER 5

ASSESSING PUBLIC ENGAGEMENT WITH SCIENCE



ASSESSING PUBLIC ENGAGEMENT WITH SCIENCE

5.1 ABSTRACT

Public engagement with science (PES) is a growing field; however, systematic assessments of PES impact are sparse. The purpose of this study was to assess the PES of the Chimpcam Project, a documentary focusing on research held on public display with the chimpanzees of Edinburgh Zoo's Budongo Trail. The documentary's reach and depth were assessed through viewership, appreciation index, web presence, visitor numbers, and a public perception survey. The project reached more than 1.2 million viewers from the initial UK broadcast (with an appreciation index of 84), 23% of the blogging world who discussed the film online, and over 8,000 unique visitors to the project website from 108 countries within the first year. Those who watched the film had a better perception of zoo research, scientists, welfare in zoos, and the importance of choice for animals. Through the documentary, web presence, visitor numbers, and public perception survey, the researchers suggest that the documentary was a successful method of public engagement with science.

5.2 INTRODUCTION

5.2.1 PUBLIC ENGAGEMENT WITH SCIENCE

Education is one of the British and Irish Association of Zoos and Aquariums' (BIAZA) main priorities for member institutions (BIAZA, 2009a & 2009b). With zoos and aquariums across the world reaching a diverse audience (Clayton & Meyers, 2009) of over 600 million visitors annually (WAZA, 2005), the outreach potential is phenomenal. To help visualise this, in the United States alone, zoo and aquarium visitors have larger audiences than the National Football League (NFL), National Basketball Association (NBA), National Hockey League (NHL), and Major League Baseball (MLB) combined (AZA, 2011).

Public engagement with science (PES), a broad "umbrella term" used to describe activities that involve sharing information about science (Crown, 2008), is regularly used as a method of education. The UK's National Co-ordinating Centre for Public Engagement (2011) describes PES as "the many ways in which higher education institutions and their staff and students can connect and share their work with the public. Done well, it generates mutual benefit, with all parties learning from each other through sharing

knowledge, expertise and skills. In the process, it can build trust, understanding and collaboration, and increase the sector's relevance to, and impact on, civil society." PES, however, goes beyond higher education institutions and is central to the aims of other institutions, such as science museums, botanical gardens and zoos (e.g. science-based facilities) aiming to engage and involve the public with their goals and activities.

PES has been promoted in various contexts for a number of years (e.g. The Royal Society, 1985), but only recently has received a great deal of attention with conferences and organisations aimed to promote and achieve PES (e.g. the Science Communication Conference from the British Science Association, Sense About Science, etc.). Despite this interest, there seems to be a social stigma attached to PES where it is viewed as an activity for those who would not be successful in academia (The Royal Society, 2006). Whether scientists would be willing to participate in PES is suggested to rely on three factors: attitude towards the engagement being positive, perception that they were in control of the engagement, and perceived participation from peers (Poliakoff & Webb, 2007).

More recently, however, major funders (e.g. RCUK) are requiring public engagement to be a component within grant proposals suggesting not only an increasing interest in it, but that those who previously frowned upon it might need to reconsider their position on the matter. Even with this increasing emphasis on, and substantial funding of PES, the systematic evaluation of science engagement activities is surprisingly limited (Garnett, 2002). In addition to funding purposes, PES has been reported (through interviews with scientists) as necessary and desirable to bridge the gap between science and the general public and contribute to the cycle of public funding by informing and engaging others (Burchell et al., 2009).

5.2.2 ASSESSING PUBLIC ENGAGEMENT WITH SCIENCE IN ZOOS

While promotion of PES has grown, effective assessments of these efforts are largely lacking. Measuring PES usually relies on the simple measure of attendance at an event or facility, but this fails to assess the levels of engagement achieved. Although evaluation is an important component in hosting any science events, the evaluation is often at a basic level (e.g. the British Science Association ask for basic demographic data and the attendees to rate the events as "enjoyable", "interesting", "informative",

“participative” and “satisfying overall” (BSA, 2011)). Whilst event organisers may use this information to improve the quality of their event in future, few meta-analyses, nor detailed studies on what components of the events are particularly successful are undertaken.

In an ideal world, enough data could be collected from participants following a PES event, as well as from control groups in additional locations; however lengthy questionnaires are not always suitable in environments which often aim to be informal and engaging when reaching out to non-traditional audiences (Rowe et al., 2005). Despite the challenges, zoos have been particularly active in assessing their own public engagement with science through modern exhibits (Birney, 1988 & 1995; Bitgood et al., 1988; Meluch & Routman 2003; Nakamichi, 2007; Ross & Gillespie, 2009); signage (Serrell, 1988), formal educational materials (Randler et al., 2007), animal training and interpretation (Swanagan, 2000; Anderson et al., 2003), and enhancing visitor knowledge (Serrell, 2001); but overall, the literature on quantifying the impact of informal education is limited (Balmford et al., 2007).

While there has been debate about the educational value of science-based facilities like zoos (with Tunnicliffe et al. (1997) pointing out a gap between the level of knowledge and interest of the visitors and the information provided by zoos), recent research has shown that visitors do demonstrate an increase in knowledge (Jensen, 2010; Wagoner & Jensen, 2010), conservation awareness (Ballantyne & Packer, 2005), positive attitudes, and understanding (Falk et al., 2007) following a zoo visit. Not only do visitors have the potential to learn from zoos, but Packer (2006) provides evidence suggesting that they attend science-based facilities (like zoos) because they seek (possibly unconsciously) a fun learning experience. In terms of attitudes towards apes, those with higher education levels viewed apes in a more positive light than those with lower levels of education, and when comparing repeat zoo visitors to first timers, the repeat visitors had more concern for the environment, the relationship between wildlife and their environment, and animal biology (Lukas & Ross, 2005).

Assessing the impact of science communication is a challenge even in terms of the short term outcomes, but it is imperative to disseminate our methodology and outcomes with the wider zoo and PES community. The approach within this chapter takes advantage of a multimedia assessment (i.e.

television and internet) where the reach and depth of the PES extends beyond (but includes) attendance.

5.2.3 EDUCATION THROUGH FILM

Nature documentaries have been used in schools and in homes for entertainment and educational purposes (Smith & Reiser, 1997). There is, without doubt, educational value in natural history films. The measurable impact of these films, however, is often under debate (Bousé, 2000; Barbas et al., 2009; Blewitt, 2010; Wright, 2010) as anecdotal evidence is often relied upon in lieu of systematic analyses (Bousé, 2000). In a rare example where the impact of nature documentaries were systematically tested on students, Barbas et al. (2009) found that after watching films about insects, the participants' emotional reactions to insects had changed for the better by becoming more knowledge-based.

5.2.4 BBC DOCUMENTARIES

5.2.4.1 NATURAL WORLD SERIES

Originally named *The World About Us* in 1967 (commissioned by David Attenborough), the series became *The Natural World* in 1983 and its focus shifted to solely natural history programmes (BBC, 2008). Operated through the BBC's Natural History Unit, episodes are shown during primetime hours on BBC TWO. As Britain's longest-running nature documentary strand, by 2011, it will have broadcast nearly 500 episodes (BBC, 2008).

The 2009/2010 *Natural World* series received an estimated average viewership of 1.76 million per episode with a 7.6% audience share each (calculated by articles from: Deans, 2009a, 2009b, 2010; Plunkett, 2009a, 2009b, 2009c, 2010; Tryhorn, 2010a, 2010b, 2010c, 2010d). This estimate includes 11 of the 14 episodes in the series due to limited ratings information.

The Appreciation Index (AI) is a score out of 100 that represents the audience's appreciation of a particular programme (BBC, 2011a). The higher the score, the higher the quality is perceived to be; an AI rating of 85 or above is considered excellent and an AI rating of 60 or below is considered poor (BBC, 2011b). GfK NOP (Growth from Knowledge National Opinion Poles), a market research company, operates the television appreciation survey by selecting participants of differing ages, gender, and

education level in order to represent the entire country (GfK Media, 2011). Knowledge-based programmes (from independent production companies) received an average AI rating of 81 in the 2009-2010 series; the same as the previous year (see Figure 5.1; Deloitte LLP, 2010). The highest rated natural history programmes received an AI rating of 93: *Life in Cold Blood* and *Tiger: Spy in the Jungle*, both narrated by Attenborough (Williams, 2008) which broadcast on BBC One, the UK's most watched channel (BBC, 2010).

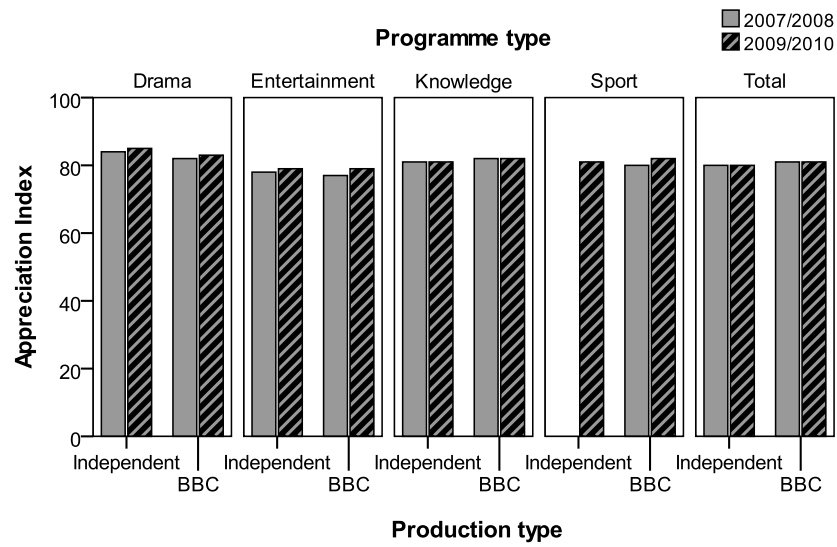


Figure 5.1. Average AI ratings by programme type, year, and production type as provided by a report for the BBC Trust (Deloitte LLP, 2010).

5.2.4.2 THE CHIMPCAM PROJECT

During the 2009/2010 series, the BBC's Natural History Unit broadcast the Chimpcam Project, an hour-long documentary from an independent wildlife filmmaker, Burning Gold Productions. Aimed at a general audience, the documentary followed the development of a chimpanzee cognitive research programme using the idea of providing the group with a chimpanzee-proof camera that they could freely take around their enclosure as an innovation to 'hook' potential viewers. In collaboration with researchers from the University of Stirling, and animal care staff from RZSS, the team developed a series of studies that would first aim to give the chimpanzees experience with video images, such as experiencing the contingency between their actions and live video feedback, for example, and allow the team to use video as a research tool to explore cognition (see Chapter 3). In addition to the development of the cognitive research programme, the team encountered dominance hierarchy

struggles within the group that allowed the filmmakers to highlight individual differences and group politics in addition to intelligence and the complex nature of conducting cognitive research with a naïve group of chimpanzees.

5.2.5 STUDY AIMS

This study aimed to assess the impact of The Chimpcam Project through the documentary's reach (viewership, appreciation index, web presence, and visitor numbers to the exhibit highlighted in the film) and depth (public perception on zoo research, scientists, welfare in zoos, and the importance of choice for animals). These concepts were explored in two analytical categories in which we identified the following questions and hypotheses:

ANALYSIS 1: REACH OF PUBLIC ENGAGEMENT

What were the documentary's (a) UK viewership, (b) Appreciation Index, and (c) presence in the blogging world?

(d) How many people visited the research website following the broadcast of the documentary?

(e) How long was the average visit to the research website?

(f) On average, how many pages did each visitor view on the research website?

(g) How many people viewed the BBC preview for the documentary on YouTube?

It was predicted that the number of visitors to (h) the zoo and (i) Budongo Trail would increase.

ANALYSIS 2: DEPTH OF PUBLIC ENGAGEMENT

The majority of those who watched the documentary would agree that from the film they (a) learned a lot about chimpanzee cognition, (b) learned more about the type of research that can be carried out within the zoo, and that (c) think chimpanzees enjoy being challenged with new research tasks⁴.

⁴ Survey statements were counterbalanced to avoid response bias (Ray, 1979). See Section 5.3.5.2 and Appendix B4 for further information.

Since the documentary was aimed at a general audience, the levels of agreement with the statements in hypotheses (a), (b), and (c), would differ based on knowledge level (referred to as hypotheses (d), (e), and (f), respectively); specifically that those with general and limited knowledge of animals and nature and of chimpanzees would have a higher mean score for each statement than those with expert knowledge (e.g. they would learn more than those with expert knowledge).

The documentary would have a positive influence on perceptions of (g) zoo research, (h) scientists, (i) welfare in zoos, and (j) the importance of choice for animals.

(k) Those who watched the documentary would be more interested in considering research as a career than those who did not (for participants under 19 years of age and are still making choices about future careers); an implicit aim of many PES endeavours, including zoos.

5.3 METHODS

5.3.1 PARTICIPANTS

A total of 391 participants took part in the anonymous public perception survey after the documentary was broadcast, representing a variety of ages and countries of residence (see Table 5.1). Self-reported knowledge levels regarding animals and nature and also chimpanzees were distributed across differing frequencies of documentary watching (see Figure 5.2) where those with higher levels of knowledge felt that people could learn a lot about animals from watching wildlife documentaries compared to those with lower levels of knowledge (Pearson's chi-square: knowledge of animals and nature, $\chi^2(2) = 42.935$, $p < 0.001$; knowledge of chimpanzees, $\chi^2(2) = 49.794$, $p < 0.001$, see Table 5.2). Of those who responded to the zoo visitation question online ($n = 163$), most reported visiting a zoo, aquarium, or science centre at least once per year during the last five years ($n = 152$). A total of 4,150 visitors to Budongo Trail and 7,823 visitors to the zoo were recorded during the period of data collection.

Table 5.1. Participant demographic information, listed by survey location.

		Online		Budongo Trail		Botanic Garden	
		n	%	n	%	n	%
Gender	Male	95	43.4	56	40.0	22	66.7
	Female	123	56.2	84	60.0	11	33.3
Age	12 and under	21	9.6	5	3.6	1	3.0
	13-19	19	8.7	24	17.1	0	0.0
	20-29	58	26.5	46	32.9	8	24.2
	30-39	36	16.4	23	16.4	3	9.1
	40-49	44	20.1	26	18.6	5	15.2
	50-59	25	11.4	8	5.7	8	24.2
	60+	15	6.8	8	5.7	8	24.2
Country of residence	UK	168	76.7	130	92.9	29	87.9
	Other	48	21.9	10	7.1	4	12.1
Group composition	Alone	NA	NA	9	6.4	10	30.3
	Adults	NA	NA	72	51.4	18	54.5
	With children	NA	NA	59	42.1	5	15.2

Table 5.2. Frequency of participant opinions on the statement, “People can learn a lot about animals from wildlife programmes”, separated by self-rated level of knowledge.

Knowledge of	Opinion categories	Self-rated knowledge level			
		Not interested	Limited	General	Expert
Animals and nature	Agree	0	15	127	43
	Disagree	3	36	131	16
Chimpanzees	Agree	1	43	115	27
	Disagree	1	108	69	8

Note: Opinions were scored on a 5 point Likert scale ranging from strongly agree to strongly disagree; Slightly and strongly agree were combined in the category of agree (the same applies for disagree); Participants who neither agreed nor disagreed and those who chose not to answer either of these questions account for differences between totals for the knowledge-based groups.

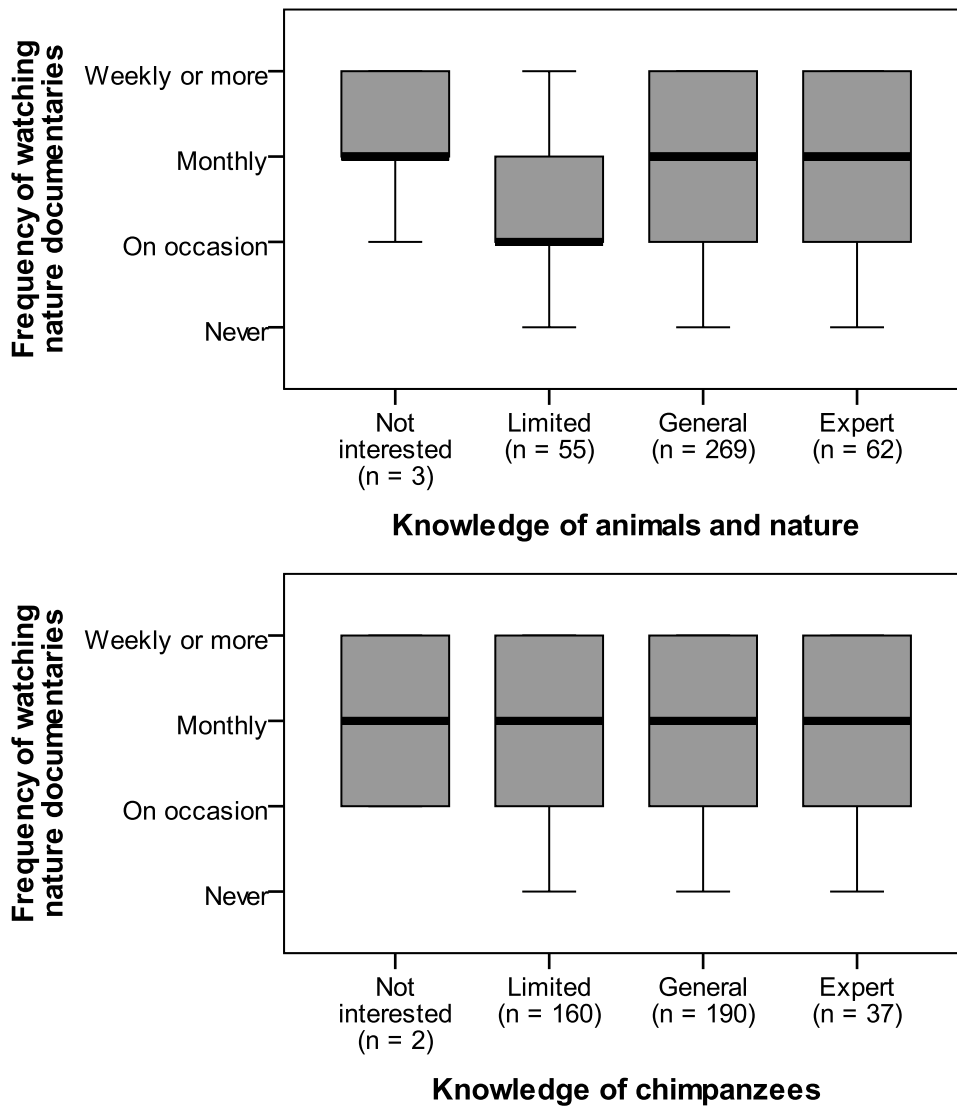


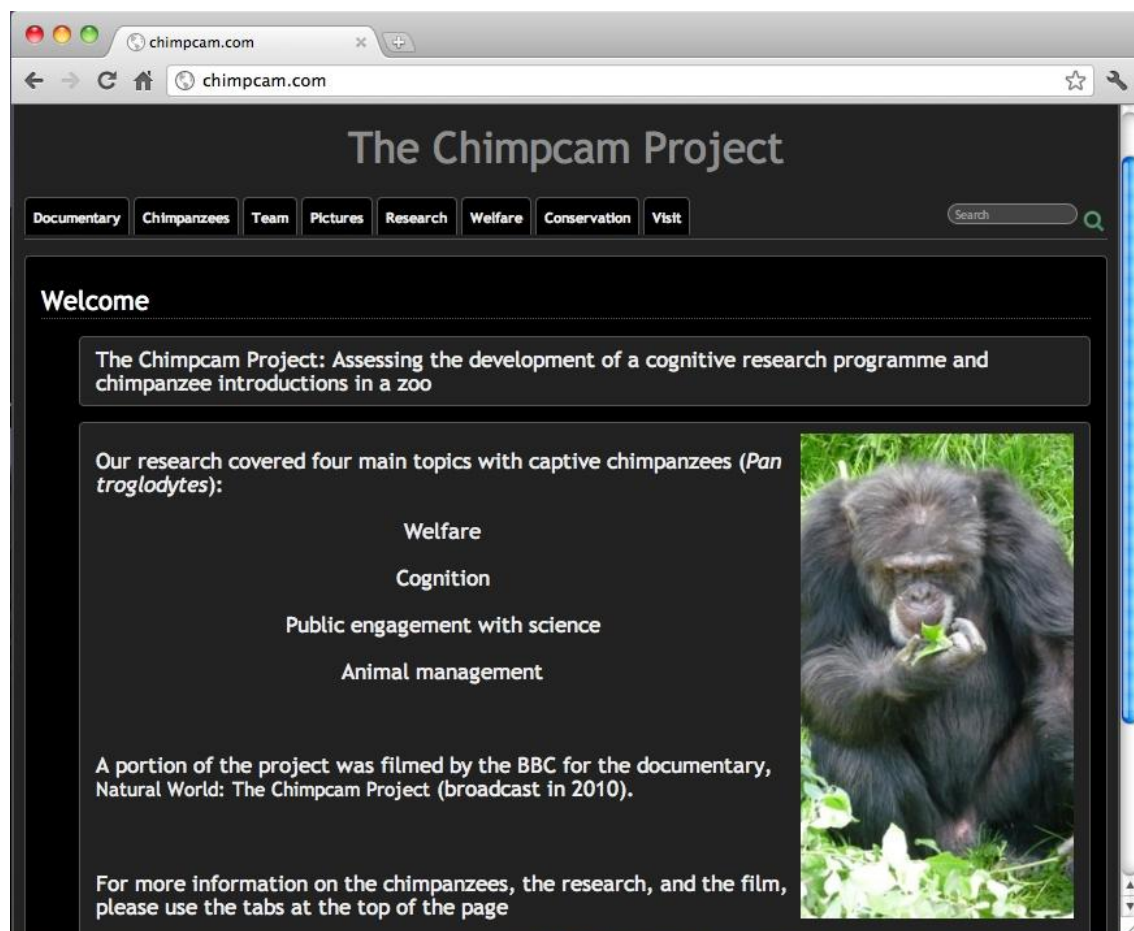
Figure 5.2. A comparison of the median and interquartile range (IQR) of the frequency of watching nature documentaries separated by knowledge of animals and nature (top) and by knowledge of chimpanzees (bottom). Whiskers represent 5th and 95th percentiles.

5.3.2 APPARATUS

A research website (www.chimpcam.com) providing details about the concept of the project and the individuals involved (see Figure 5.3) and a BBC preview of the documentary on YouTube (http://www.youtube.com/watch?hl=en&v=RH4_2IZ3vb8&gl=US) were used to promote the project and documentary (see Figure 5.7). Google Analytics was used to identify demographics of visitors to the research website and Pew Research Center's Project for Excellence in Journalism New Media Index (www.journalism.org) was used to identify blogging statistics. Paper (see Appendix B4) and online

(hosted by Survey Monkey) surveys with identical Likert-scale questions were used to collect data, with the exception of the in-person surveys which also recorded data on visitor group composition and whether or not they had visited the project website. The survey scored a 6.9 on the Flesch-Kincaid Grade Level suggesting that 11-year-old children would be able to read the questions with ease. BPS ethical guidelines for research with human participants were adhered to (BPS, 2010). Information sheets were used to inform participants that their completion of the survey served as consent to participate and to remind paper survey participants of the response options (see Appendix F1), and business cards highlighting the project were used to offer debriefing information (see Appendix F2). Paper checksheets (see Appendix B5) were also used to collect information on the visitors to Budongo Trail (visitor numbers, age, and sex).

Figure 5.3. The Chimpcam Project research website (www.chimpcam.com).



5.3.3 MEASURES AND COMPARISONS

Documentary viewership, Appreciation Index, web presence, and visitor numbers to Budongo Trail and the zoo (before and after the broadcast) were collected and public perception was surveyed following the UK broadcast of the documentary, *The Chimpcam Project* (BBC) on 27 January 2010. Surveys included reverse-coded questions to control for response bias (Ray, 1979) and were conducted in three different venues: Budongo Trail (the chimpanzee exhibit highlighted in the film), online (hosted by Survey Monkey), accessible by a link on the project website (www.chimpcam.com), and Edinburgh's Royal Botanic Gardens (a control site to reach individuals who were interested in science and nature, but did not necessarily visit the zoo; as watching the documentary or visiting the zoo already suggests an interest in animals). While the survey locations were different, to reach a wide range of participants, each represented individuals who made an effort to participate in a science-related activity. The participants' opinions were similar across the main categories of interest. See Table 5.3 for survey details in each testing location.

Table 5.3. Survey details by location: Online, Budongo Trail, and the Botanic Garden.

Location	Dates administered	Number of surveys	Median participant opinion of key research questions (see Table 5.4)			
			Zoo Research	Scientists	Welfare	Choice
Online	28 January 2010 – 12 May 2011	218	5	4.5	5	5
Budongo Trail	28 January – 13 February 2010	140	4.5	4.5	5	5
Botanic Garden	25 – 26 February 2010	33	5	4.5	5	5

5.3.4 DATA COLLECTION

Visitor data within Budongo Trail were collected during the zoo's opening hours by the researcher and zoo volunteers ($n = 16$) from 20 January – 7 February 2010 with the exception of 22 January which was omitted due to no staff availability. The size and composition of each group visiting Budongo Trail was recorded noting the age of each individual (gender was recorded but omitted because of low reliability amongst children 12 and under). Overall visitor data to the zoo was provided by RZSS's visitor services department.

Since weather has been known to impact zoo-visitor volume, with an increase in nice weather and decrease in bad weather (Davey, 2007), overall weather (e.g. cloudy) was recorded by the researcher on a daily basis and temperature and humidity data were extracted from a historical database from, Weather Underground (www.wunderground.com); an online reporting service developed by the University of Michigan in 1991. See Appendix F3 for weather reported during this study.

Surveys completed in Budongo Trail and in the Botanic Gardens were administered in person by survey guides (the researcher or volunteers, $n = 12$) who read aloud the informed consent statement and survey questions to each participant and then recorded their responses. Survey guides also recorded each participant's group composition. All visitors to Budongo Trail and the Botanic Gardens (in the Gateway visitor centre) had equal opportunity to participate in the survey during the opening hours of each facility (09:00 – 16:00 for Budongo Trail and 10:00 – 16:00 for the Botanic Gardens) within the test dates for each location (see Table 5.3). Participants were selected at random; however, any participants who were greatly outnumbered by children in their group or were generally preoccupied with those in their care (e.g. chaos management, feeding, etc.) were excluded. For continuity purposes, survey guides were briefed at the start of their participation on the methodological approach for this study.

5.3.5 DATA ANALYSIS

5.3.5.1 REACH OF PUBLIC ENGAGEMENT

The documentary's viewership (number of viewers) and web presence were analysed with descriptive statistics (frequency of occurrence and percentage of links). Visitor numbers to Budongo Trail and the zoo were analysed with controls in place to accurately assess any changes in visitor numbers due to the broadcast of the documentary (i.e. school groups were omitted from analyses as their visits were likely planned prior to the broadcast and similar weather conditions were compared as these are known to impact visitor numbers, see Appendix F3).

5.3.5.2 DEPTH OF PUBLIC ENGAGEMENT

All survey statements and responses were adjusted for analyses so that each item was positively phrased (i.e. "I am interested in watching the scientists at work within the zoo" as opposed to the actual statement on the survey, "I am not interested in watching the scientists at work within the zoo."). Four

primary areas on interest (see Table 5.4), identified by the researchers, were extracted from the survey responses because the principal component analysis (PCA) revealed only one factor, explaining 70.83% of the variance, after demographic and background data were omitted (Field, 2009).

Table 5.4. Four categories of interest from the survey with their corresponding questions (see Appendix B4), reverse coded with questions positively worded.

Categories	Survey Questions
Zoo Research	(Q16) I think it is a good idea for zoos to host research with chimpanzees. (Q20) I am likely to visit a zoo that is involved in research.
Scientists	(Q17) I am interested in watching the scientists at work within the zoo. (Q18) I would like to be able to talk to scientists working in the zoo.
Zoo Welfare	(Q25) Animal welfare in zoos has changed in the past 20 years.
Choice	(Q21) Animals should have a choice when it comes to participating in research.

5.3.5.3 INTER-OBSERVER RELIABILITY

Inter-observer reliability was tested between the researcher and each volunteer ($n = 17$) for a duration of at least 15 minutes. The following categories reached acceptable levels of inter-observer reliability (group means reported): group size ($r = 0.99$, range: 0.93 – 1.0), adults ($r = 0.97$, range: 0.77 – 1.0), children under 12 years old ($r = 0.95$, range: 0.84 – 1.0), and children 13-18 years old ($r = 0.99$, range: 0.87 – 1.0), see Appendix F4.

5.4 RESULTS

5.4.1 ANALYSIS 1: REACH OF PUBLIC ENGAGEMENT

DOCUMENTARY VIEWERSHIP, APPRECIATION, AND WEB PRESENCE

Based on the initial UK broadcast (27 January 2010), (a) approximately 1.2 million viewers representing a 5% audience share watched the documentary (Tryhorn, 2010a) with (b) an Appreciation Index of 84 (J. Capener, personal communication, 2010). The documentary was the most frequently mentioned topic in the blogging world with (c) 23% of all blog links discussing the film during the week of the broadcast (see Figure 5.4; PEJ, 2010). Within the year following the broadcast of the documentary, (d) the research website was visited by 8,191 unique visitors (i.e. each visitor is only counted once, regardless

of repeat visits) from 108 countries (see Figure 5.5). Visitor numbers (recorded by Google Analytics) increased following press coverage of the documentary in TV magazine programme listings (available on 22 January 2010, see Figure 5.6) and numerous newspaper, magazine, television, and radio interviews that occurred within the following days, with the site having visitors every day from 22 January 2010 through 30 May 2011 (bar 25 December 2010). The research website had (e) an average visit length of 2 minutes and 29 seconds with (f) an average of 3.55 pages (out of 39 total pages) viewed per visit. Within the year following the broadcast of the documentary, (g) the official BBC documentary preview was viewed 172,460 times on YouTube (see Figure 5.7).

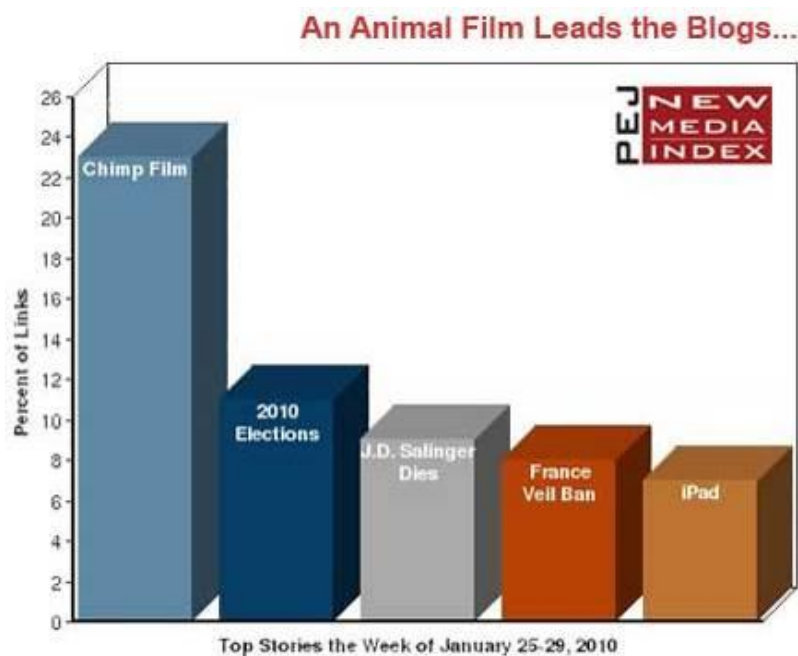


Figure 5.4. Topics with the highest percentage of blog links during 25-29 January 2010 according to the Project for Excellence in Journalism New Media Index. The percentage of links were calculated by PEJ using Icerocket, an internet tracking website, which calculates the number of blogs containing links to articles or websites (PEJ, 2010).

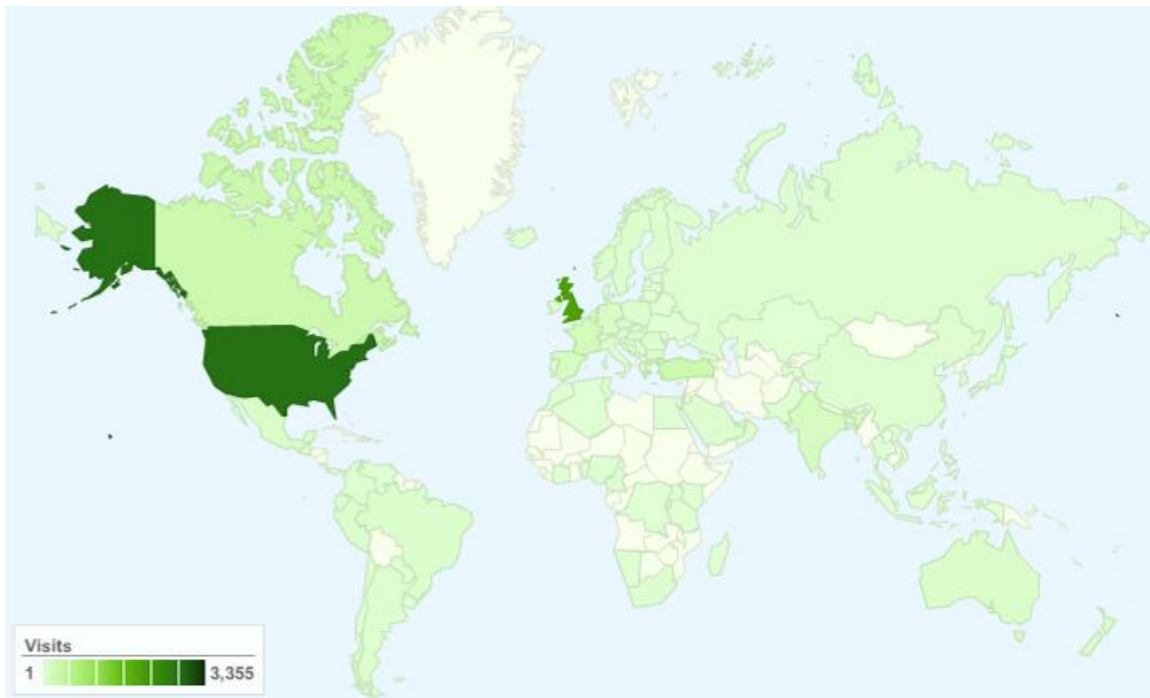


Figure 5.5. Visitors to chimpcam.com, by country from 22 January 2010 – 27 January 2011 (provided by Google Analytics).

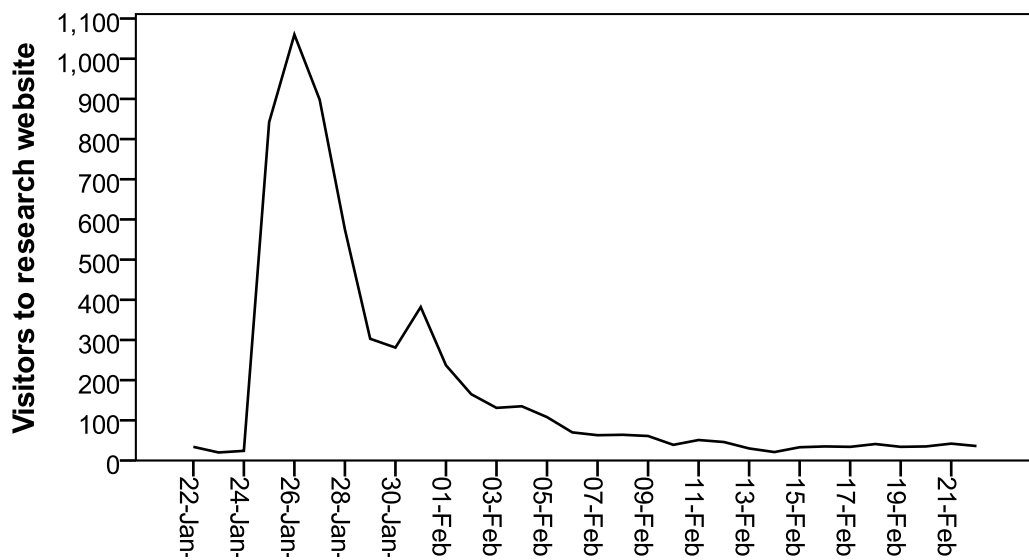


Figure 5.6. Visits to Chimpcam.com from 22 January – 23 February 2010 (provided by Google Analytics).

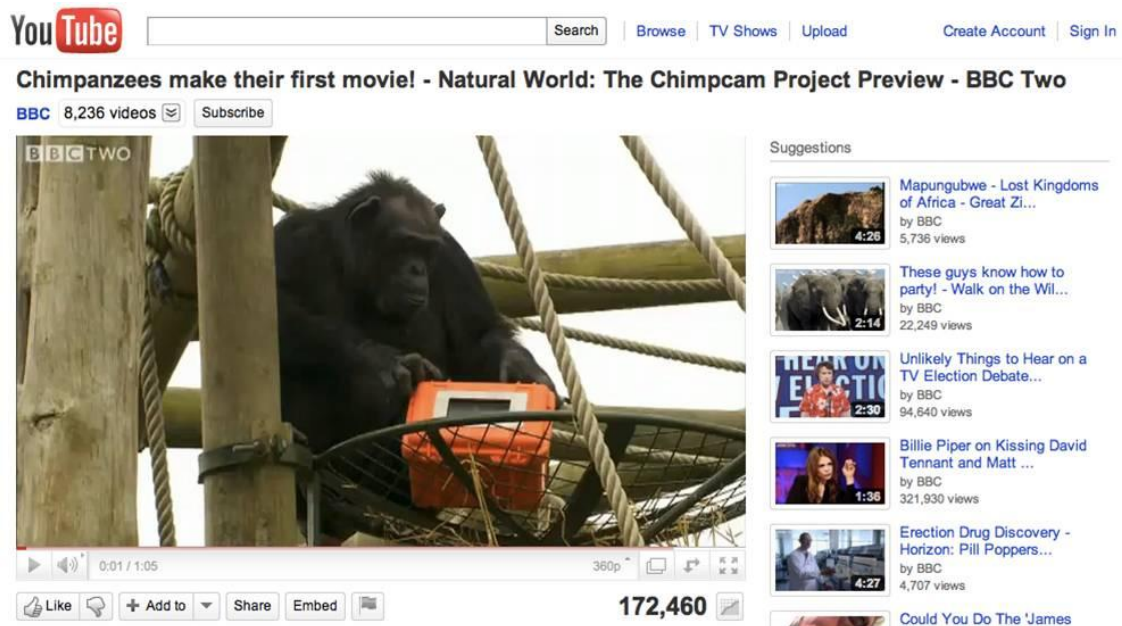


Figure 5.7. BBC preview of the documentary on YouTube with 172,460 views within one year of the initial broadcast.

VISITORS TO EDINBURGH ZOO AND BUDONGO TRAIL

Visitors to (h) the zoo and (i) Budongo Trail (see Table 5.5) did not significantly increase following the broadcast of the documentary⁵: Zoo before (mean = 523.71, SE mean = 117.25) and after (mean = 884.00, SE mean = 295.47; Independent samples t-test with transformed data, $t(12) = -1.011$, $r = 0.28$, $p = 0.33$, $n = 14$, see Figure 5.8): and Budongo Trail before (median = 140.0) and after (median = 257; Mann-Whitney U Test, $U = 36$, $z = 1.469$, $p = 0.142$, $r = 0.39$, see Figure 5.9):

⁵ Given the nature of the weather during the week prior to the broadcast, additional analyses were performed where the four days immediately following the broadcast, 28-31 January, were omitted due to unseasonably nice weather which may have inflated visitor numbers, unrelated to the broadcast. When controlling for weather, the results remain the same, nonsignificant.

Table 5.5. Total visitor numbers and percent increase for RZSS's Edinburgh Zoo and Budongo Trail before and after the broadcast.

Category	Week Before	Week After	% Increase
Edinburgh Zoo	3,666	4,157	13.39
Budongo Trail	1,874	2,276	21.45

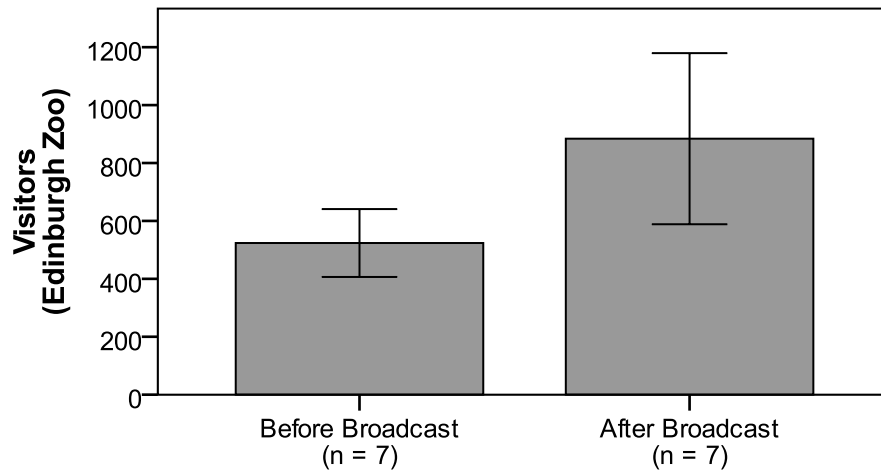


Figure 5.8. A comparison of the mean (\pm 1 SE) number of visitors per day to RZSS's Edinburgh Zoo one week before and after the broadcast.

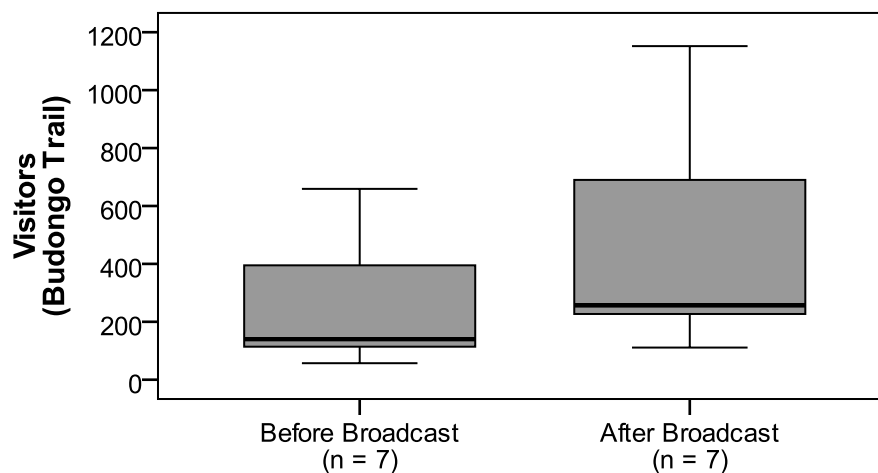


Figure 5.9. A comparison of the median and interquartile range (IQR) of the number of visitors per day to Budongo Trail one week before and after the broadcast. Whiskers represent 5th and 95th percentiles.

5.4.2 ANALYSIS 2: DEPTH OF PUBLIC ENGAGEMENT

SURVEY: THE CHIMPCAM PROJECT

Of the 389 participants who identified whether or not they saw the Chimpcam Project, 169 (43.4%) reported seeing the documentary (sample sizes of those who watched the documentary versus those who did not may differ in the following analyses due to participant response rate for each specific variable being compared). In accordance with the hypothesis, the majority agreed (sum of slightly agree and strongly agree) that (a) they learned a lot about chimpanzee cognition (81.33%), (b) they learned more about the type of research that can be carried out within the zoo (88.67%), and (c) they think chimpanzees enjoy being challenged with new research tasks (51.33%), see Figure 5.10.

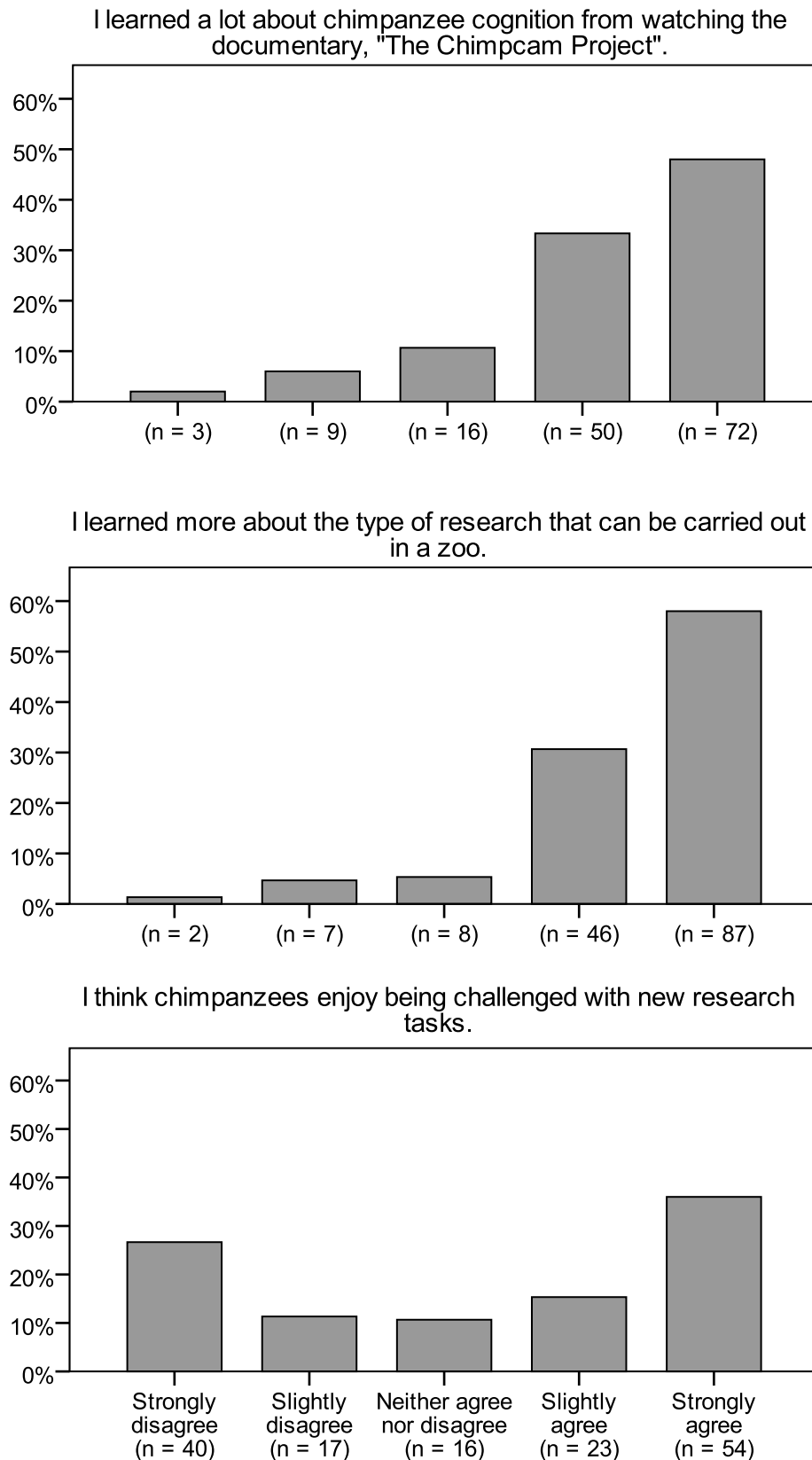


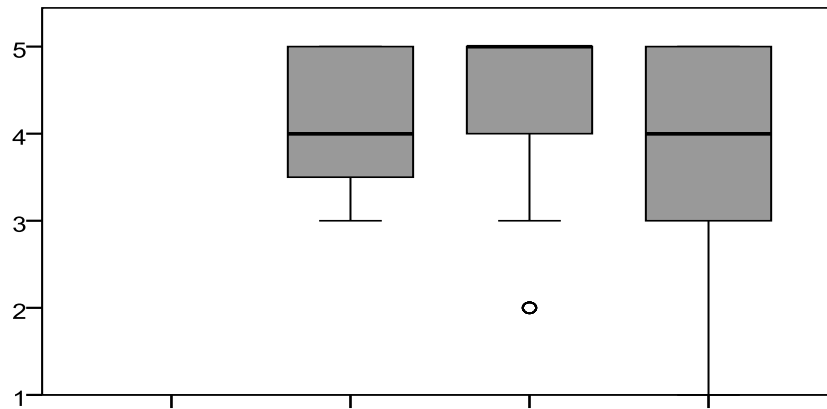
Figure 5.10. Percentage of Likert scale agreement for survey questions 13 (top), 14 (middle), and 15 (bottom).

Since the documentary was aimed at a broad audience, the statements from the previous analysis were analysed in terms of self-reported knowledge level, in relation to differences between expert and non-experts. There was no significant difference across (d) animal and nature knowledge levels for the statement, I learned a lot about chimpanzee cognition (Kruskal-Wallis test, $H = 4.73$, $p = 0.09$, $n = 149$, see Figure 5.11): Expert (median = 4.0, $n = 29$), general (median = 5.0, $n = 104$), limited (median = 4.0, $n = 16$), and not interested ($n = 0$), however, there was a significant difference for the chimpanzee knowledge levels (Kruskal-Wallis test, $H = 8.04$, $p = 0.02$, $n = 150$, see Figure 5.12): Expert (median = 4.0, $n = 20$), general (median = 5.0, $n = 87$), limited (median = 4.0, $n = 43$), and not interested ($n = 0$). One follow-up test reached the adjusted significance value (0.0167): Individuals with general knowledge learned more than those with expert knowledge (Mann Whitney U, $U = 1,196.0$, $z = 2.82$, $p = 0.005$, $r = 0.27$, $n = 107$). There was no statistical difference in self reported learning between those with expert and limited knowledge ($U = 566.0$, $z = 2.14$, $p = 0.03$, $r = 0.27$, $n = 63$), nor was there a difference between those with general and limited knowledge ($U = 1,755.0$, $z = -0.63$, $p = 0.53$, $r = -0.05$, $n = 130$) as the data did not reach the adjusted significance value.

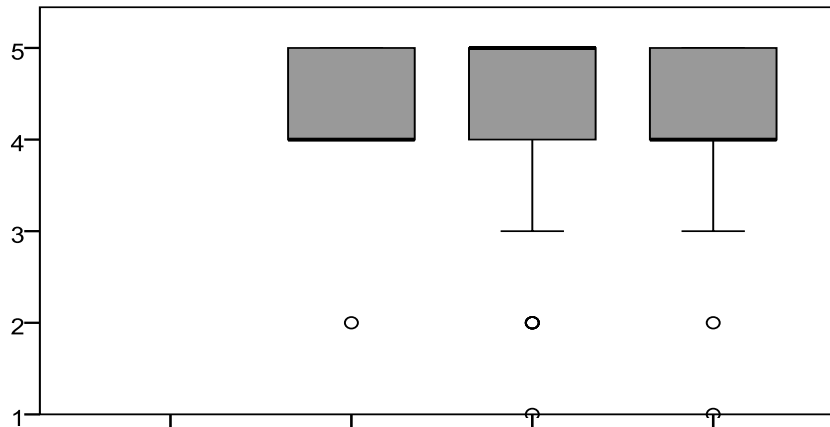
There were no significant differences across (e) animal and nature knowledge levels for the statement, I learned more about the type of research that can be carried out within the zoo (Kruskal-Wallis test, $H = 2.78$, $p = 0.25$, $n = 149$, see Figure 5.11): Expert (median = 4.0, $n = 29$), general (median = 5.0, $n = 104$), limited (median = 4.0, $n = 16$), and not interested ($n = 0$). Nor were there differences across chimpanzee knowledge levels (Kruskal-Wallis test, $H = 1.73$, $p = 0.42$, $n = 150$, see Figure 5.12): Expert (median = 4.0, $n = 20$), general (median = 5.0, $n = 87$), limited (median = 5.0, $n = 43$), and not interested ($n = 0$).

There were no significant differences across (f) animal and nature knowledge levels for the statement, I think chimpanzees enjoy being challenged with new research tasks (Kruskal-Wallis test, $H = 1.41$, $p = 0.49$, $n = 149$, see Figure 5.11): Expert (median = 4.0, $n = 29$), general (median = 4.0, $n = 104$), limited (median = 2.5, $n = 16$), and not interested ($n = 0$). Nor were there significant differences across chimpanzee knowledge levels (Kruskal-Wallis test, $H = 2.27$, $p = 0.32$, $n = 150$, see Figure 5.12).

I learned a lot about chimpanzee cognition from watching the documentary, “The Chimpcam Project”.



I learned more about the type of research that can be carried out within the zoo.



I think that chimpanzees enjoy being challenged with new research tasks.

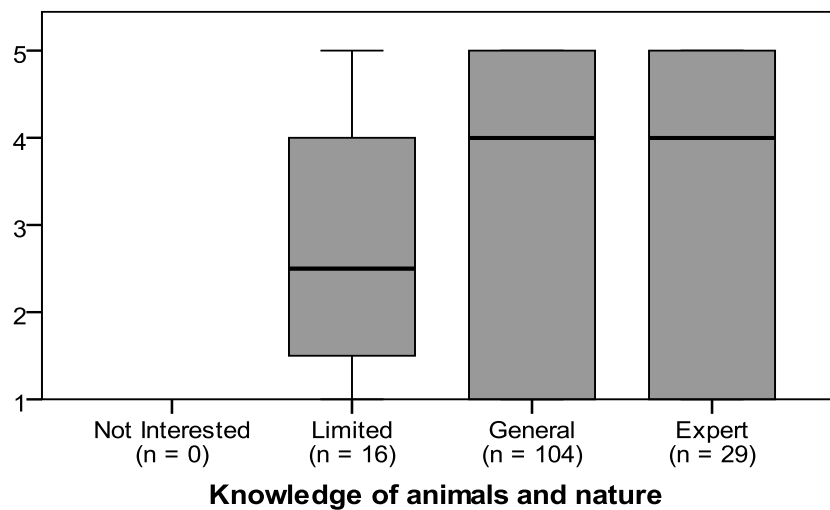
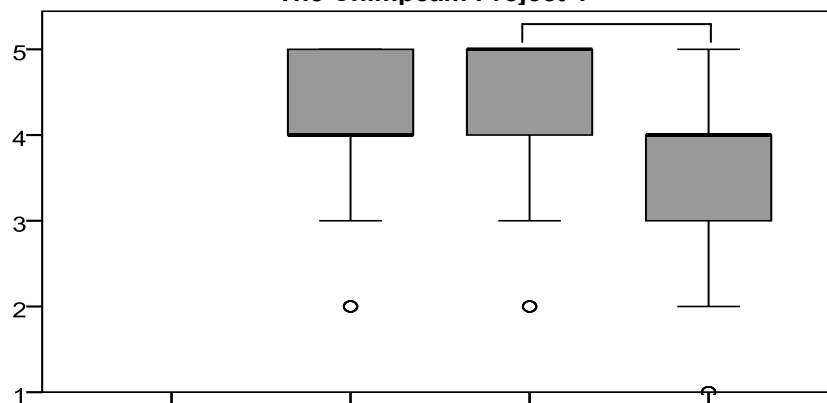
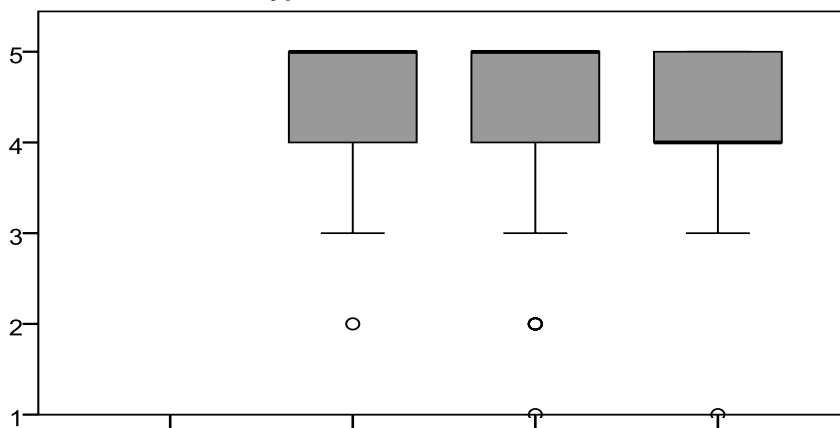


Figure 5.11. A comparison of the median and interquartile range (IQR) of Likert scale participant scores on questions about the documentary by level of knowledge of animals and nature. Whiskers represent 5th and 95th percentiles; circles represent outliers.

I learned a lot about chimpanzee cognition from watching the documentary, “The Chimpcam Project”.



I learned more about the type of research that can be carried out within the zoo.



I think that chimpanzees enjoy being challenged with new research tasks.

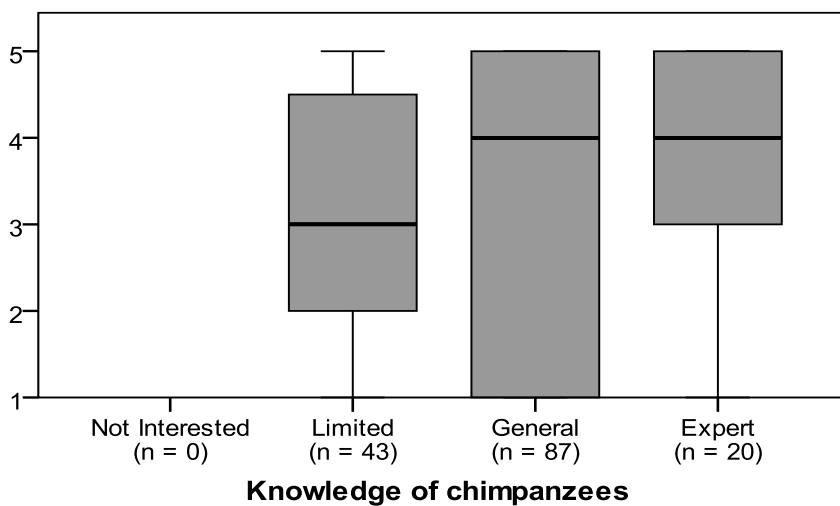


Figure 5.12. A comparison of the median and interquartile range (IQR) of Likert scale participant scores on questions about the documentary by level of knowledge of chimpanzees. Whiskers represent 5th and 95th percentiles; circles represent outliers; adjoining brackets highlight significant differences.

Compared to those who did not watch the documentary, those who watched had similar perceptions of zoo research, welfare in zoos, and the importance of choice for animals. Those who watched the documentary had a more positive perception of scientists (see Figure 5.13): (g) zoo research (Mann-Whitney U test, $U = 15,095.0$, $z = 0.032$, $r = 0.002$, $p = 0.975$, $n = 352$): watched (median = 5.0, $n = 147$) and did not watch (median = 5.0, $n = 205$); (h) scientists ($U = 17,973.0$, $z = 3.192$, $r = 0.17$, $p = 0.001$, $n = 352$): watched (median = 4.5, $n = 147$) and did not watch (median = 4.5, $n = 205$); (i) welfare in zoos ($U = 14,890.0$, $z = 0.09$, $r = 0.005$, $p = 0.93$, $n = 349$): watched (median = 5.0, $n = 146$) and did not watch (median = 5.0, $n = 203$); and (j) the importance of choice for animals ($U = 15,741.0$, $z = 0.942$, $r = 0.05$, $p = 0.35$, $n = 351$): watched (median = 5.0, $n = 147$) and did not watch (median = 5.0, $n = 204$).

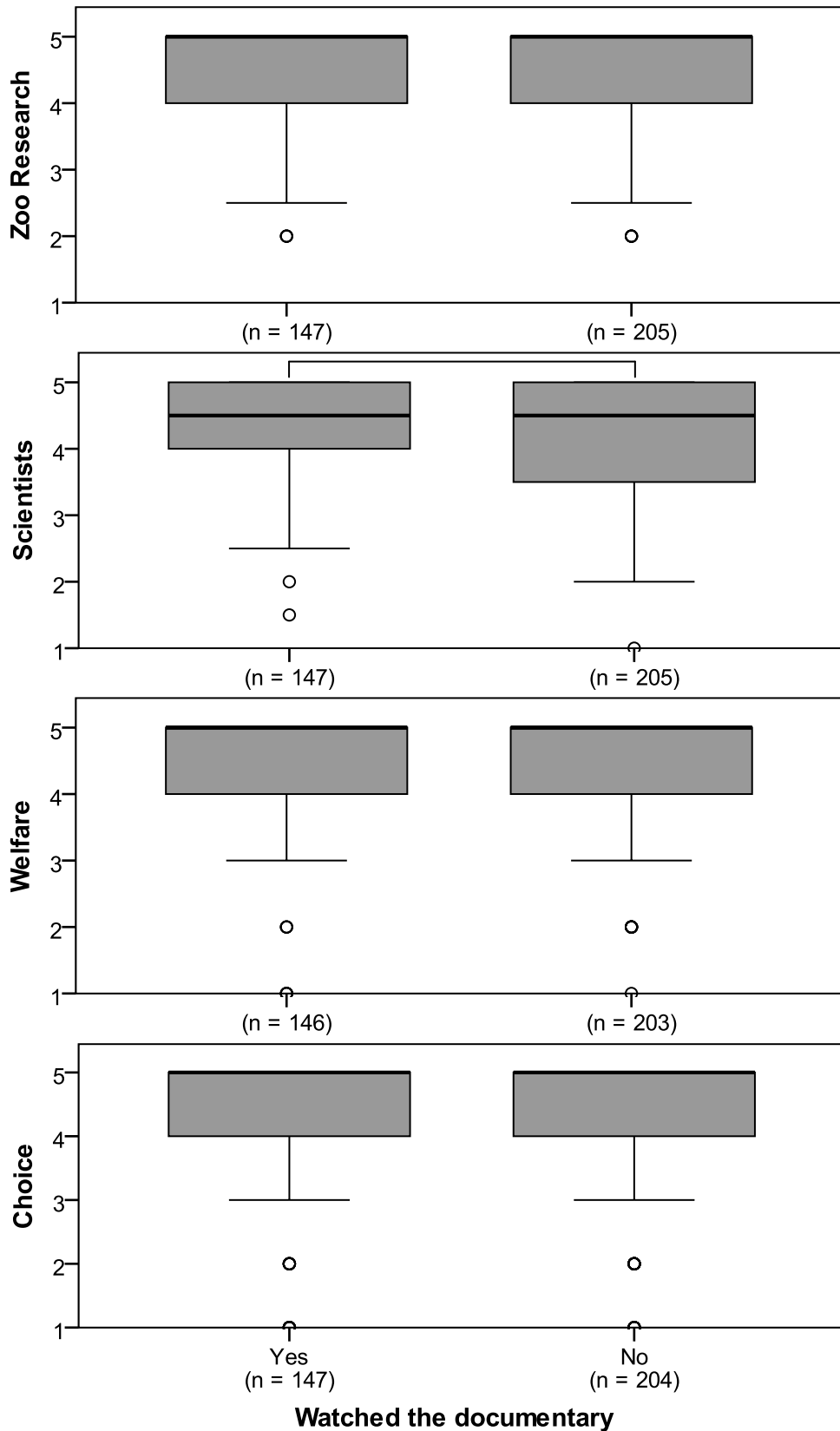


Figure 5.13. A comparison of the median and interquartile range (IQR) of perception of zoo research, scientists, welfare and choice by status of watching the documentary. A Likert scale of 1 (strongly disagree) to 5 (strongly agree) was used to gauge responses for each topic. Whiskers represent 5th and 95th percentiles; adjoining bracket highlights significant differences.

SURVEY: DOCUMENTARY LINK TO CAREER CHOICE

(k) When analysing participants under 19 years old, there was no significant difference in considering research with animals as a future career based on whether or not they watched the documentary (Mann-Whitney U test, $U = 407.0$, $z = 0.51$, $r = 0.07$, $p = 0.61$, $n = 55$, see Figure 5.14): watched (median = 4.0, $n = 27$) and did not watch (median = 4.0, $n = 28$).

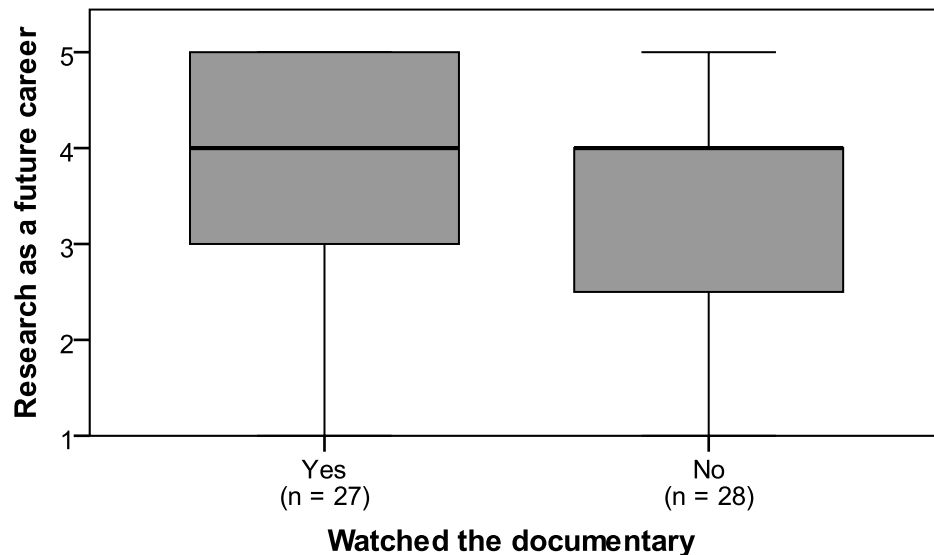


Figure 5.14. A comparison of the median and interquartile range (IQR) of levels of agreement in considering research with animals as a future career by status of watching the documentary. A Likert scale of 1 (strongly disagree) to 5 (strongly agree) was used to gauge responses for each topic. Whiskers represent 5th and 95th percentiles.

5.4.3 SUMMARY OF RESULTS

Between the first UK broadcast (27 January 2010) and the BBC iPlayer, the Chimpcam Project reached 2 million viewers with an AI of 84 out of 100. The week of the broadcast the documentary was the most blogged about topic with 23% of all blog links mentioning the film (PEJ, 2010) showing that the programme had excellent reach. During the year following the broadcast 8,191 unique visitors from 108 countries visited the research website (www.chimpcam.com) and the BBC documentary preview was viewed 172,460 times on YouTube. The mean number of visitors to Edinburgh Zoo and Budongo Trail the week before and after the broadcast did not significantly differ.

In terms of the depth of the PES, the survey revealed that the majority of those who watched the documentary agreed that they learned a lot about chimpanzee cognition, learned more about the type of research that can be carried out within the zoo, and think that chimpanzees enjoy being challenged with new research tasks. While perceptions of zoo research, welfare, and the importance of choice were

similar regardless of whether or not participants watched the documentary, those who watched the documentary were more likely to have better perceptions of scientists. When considering research with animals as a future career, participants 19 years of age and under, who watched the documentary, did not differ from those who did not see it.

5.5 DISCUSSION

5.5.1 REACH OF PUBLIC ENGAGEMENT

5.5.1.1 DOCUMENTARY VIEWERSHIP, APPRECIATION, AND WEB PRESENCE

Based on the initial UK broadcast alone, the approval index for the Chimpcam Project was higher than average for all programming types (Deloitte LLP, 2010). The combination of a high AI with the lower-than-average viewer numbers suggest that the audience was mostly built of core fans rather than having wider appeal. This could mostly be due to the scheduling conflict between the initial broadcast and two other programmes which received the bulk of the ratings (J. Capener, personal communication, 2011), the return of a new episode of ITV's *Midsomer Murders* (5.8m viewers with 23% audience share) and the Manchester City versus Manchester United Carling Cup semifinal football match (2.2m viewers with a 9% audience share, Tryhorn, 2010a). The documentary was popular enough, however, to be repeated within the UK and broadcast in several other countries. The other broadcasting countries that the researchers were aware of at the time of printing were: Canada (Bell Media, 2010), the United States (Animal Planet, 2011), Denmark (S. Romer, personal communication, 2010), the Netherlands (W. Bruijn, personal communication, 2010), and Portugal (S. Costa, personal communication, 2011).

Moreover, the documentary had impact beyond its initial broadcast on television. In order to assess the documentary's reach beyond the broadcast itself, the researchers looked at interest shown on the internet. A plethora of newspaper and magazine articles and television and radio interviews no doubt sparked the international interest with the most discussion coming from an unexpected source, blogs. In the blogging world, the documentary was the most frequently mentioned topic with 23% of all blog links discussing the film; the nature of the content within the blogs was not disclosed (i.e. whether or not the comments were positive or negative). The Chimpcam Project overshadowed discussion of the United States 2010 elections and Apple's iPad release (which occurred on the same day as the

documentary's initial broadcast); an impressive achievement from the perspective of the researchers and production team.

Two different methods of online outreach were used to inform the public about the project: a research website (www.chimpcam.com) and a minute-long preview of the film on YouTube. Both promoted the film and the project, but in different ways: the information-based research website provided details about the concept of the studies and the individuals involved while the YouTube preview provided a brief clip of the film showing what the chimpanzees did with the camera provided (the chimpcam). Drawing in different audiences, as expected, the YouTube clip was appealing to a larger audience (172k views) compared to the website's smaller audience (8k unique visitors with 32k page views). In contrast to the minute-long YouTube clip, visitors to the research website viewed multiple pages (average 3.55 pages per visitor) and remained on the site for a longer period of time (average 2m 29s) suggesting that the different outreach methods were effective in their own way of project promotion. The international interest in the project was reflected in visitor numbers to the research website. During the year following the broadcast visitors in 108 countries viewed the website. The primary (documentary) and supplementary (websites) methods of PES allowed us to reach audiences that go beyond the academic environment and meet their needs in terms of individual goals. By searching for Chimpcam on the internet, those who wanted a quick peak at the footage the chimpanzees filmed themselves could select the brief YouTube clip, while those who were interested in more detailed information, could select the project website to learn more (some of whom went one step further and emailed the primary researcher to express enthusiasm for the project and ask questions).

5.5.1.2 VISITORS TO EDINBURGH ZOO AND BUDONGO TRAIL

Visitor numbers to Edinburgh Zoo and Budongo Trail did not differ before and after the broadcast, but since there are other reasons to believe the documentary had a wide reach as a PES method, this could be due to other reasons. Many factors play a role in the decisions the public make about where they go and how they spend their money. The time periods examined focused on the week immediately before and after the documentary broadcast and if people who saw the film were inspired to visit the zoo, they might not have done so right away since zoo visits are generally day-long events that can be costly.

Although attendance to an event has been used as a fairly easy way to assess impact, this suggests that it should not be the sole measure when assessing PES.

5.5.2 DEPTH OF PUBLIC ENGAGEMENT

The use of a survey allowed the researchers to learn more about the influence the documentary had on the perception of zoo research, scientists, welfare in zoos, and the importance of choice, links between the documentary, knowledge and career choice, and the impact of visiting science-based facilities.

5.5.2.1 THE CHIMPCAM PROJECT

While the impact of wildlife films on the public has been discussed by many, systematic studies have been lacking (Blewitt, 2010). The majority of those who watched the documentary agreed that they learned a lot about chimpanzee cognition, learned more about the type of research that can be carried out within the zoo, and think chimpanzees enjoy being challenged with new research tasks. This suggests that not only was the documentary watched, but the majority of the participants who saw it took away the main messages intended. The knowledge of the participants (for animals and nature and for chimpanzees) had no bearing on the level of agreement suggesting that even though the film was created for a general audience, it worked well for various audiences.

“Research with animals” is a phrase that may conjure images of in-vivo experimentation (Herzog, 1995) when in fact there are different types of research (Hosey et al., 2009) that are non-invasive and either voluntary (i.e. cognitive research) or unobtrusive to the animal (i.e. observational, Dawkins, 2007). By creating a documentary with a rare look into the often challenging nature of behavioural research with animals, the viewers could see that “research with animals” can be a positive phrase. For several aspects of research with animals that were included in the film (i.e. research, welfare in zoos, and the importance of choice), there were no differences between those who watched and those who did not. This indicates that those who took the initiative to participate in a science-related activity (visit the zoo, botanic garden, or a website about behavioural research with chimpanzees), already had positive perceptions of the highlighted features. The difference in participant interest in watching scientists at work, and having the opportunity to talk to them, suggests that although those who watched already had high perceptions of research, the film might have had a positive influence on their opinions of

scientists. Additional focus-group research capturing before and after opinions in relation to watching the film would help to clarify causal relationships, if any.

Action beyond visiting Edinburgh Zoo and Budongo Trail was not addressed in this study, but in accordance with Senegalese Environmentalist Baba Dioum's 1969 speech to the general assembly of the IUCN in New Dehli, India, "In the end, we will conserve only what we love. We will love only what we understand. We will understand only what we are taught." Measuring the impact of wildlife documentaries on public perception is the first step to conserving the animals that are the focus of our research and our films. To encourage the world to care for animals and nature by sharing what we, those who work closely with animals, find most fascinating is an ideal start.

5.5.2.2 DOCUMENTARY LINK TO KNOWLEDGE AND CAREER CHOICE

Self assessment of knowledge was distributed differently, dependent upon the topic. More individuals felt they had a higher level of knowledge regarding animals and nature compared to chimpanzees specifically. As the topic of animals and nature is broader than the topic of chimpanzees, one might expect fewer individuals to claim expert knowledge of the latter. Participants who rated themselves as having higher levels of knowledge watched documentaries more frequently and the higher their knowledge, the more they agreed that people could learn more about animals from watching wildlife programmes. This supports the concept that wildlife documentaries have an educational value in that they impart knowledge onto others, or simply attract individuals who already have knowledge on a particular subject; we cannot know the direction of this relationship based on this study. In the case of the Chimpcam Project, the viewership and AI ratings would suggest that the film attracted those who already had knowledge on a particular subject, but to simplify it to those terms would overlook its value. The visitor numbers to Edinburgh Zoo and Budongo Trail as well as the higher agreement with key message from the film (regardless of knowledge level) suggest that the documentary appealed to individuals with varied levels of knowledge.

In considering future careers, children 19 years of age and under are the most impressionable. The documentary, in this instance did not have any bearing on considering research as a future career. Survey participants 19 years of age and under, who saw the documentary did not differ from those who

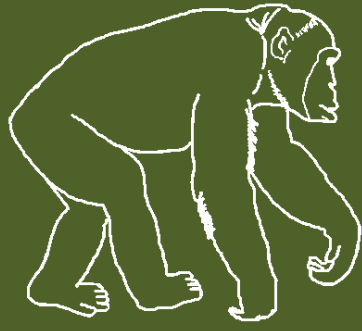
did not see it in considering research with animals as a future career. A variety of career fields have the opportunity to work closely with animals and science. Given the large increase in this age group's visits to Budongo Trail, perhaps the question was too limited by asking only about research with animals rather than the broader categories of research or working with animals.

5.5.2.3 SURVEY LOCATIONS AND THE IMPACT OF SCIENCE-BASED FACILITIES

There has been debate about the educational value of science-based facilities like zoos (Tunnicliffe et al., 1997). More recent research, however, has shown that visiting a zoo can have direct benefits to knowledge (Wagoner & Jensen, 2010). Surveying individuals in different locations (online, in a zoo, and in a botanic garden) suggest that those visiting science-based facilities had just as favourable perceptions of our items of interest (i.e. zoo research, scientists, welfare, and the importance of choice) compared to online participants. However, the great majority of online participants have regularly visited at least one science-based facility in the past five years, so while our data set differed based on survey location, it was not due to the location itself. Additionally, participation online required individuals to not only want to participate, but also to seek out the survey, suggesting that the online audience represented individuals who were keen to become involved in an animal-related activity even if they were not able to visit Edinburgh Zoo.

5.6 SUMMARY AND CONCLUSIONS

The Chimpcam Project was the first large-scale research project for the chimpanzees of Budongo Trail and the documentary was a first for Edinburgh Zoo. Public engagement generally reaches those who are already engaged, so outreach is often limited. Through the documentary, web presence, visitor numbers, and public perception survey, the researchers suggest that the documentary was a successful method of public engagement with science in terms of both reach and depth. The methods used went beyond the scope of short-term analyses with visitor numbers and evaluated opinions in relation to the film. By glimpsing into the minds of the general public we can begin to look at the long-term impact of our PES and develop future methods to identify how we might meet the public's needs to further our goal of science awareness and ultimately conserving the species we study.



CHAPTER 6

BEHAVIOURAL PREDICTORS OF INTRODUCTION OUTCOMES



BEHAVIOURAL PREDICTORS OF INTRODUCTION OUTCOMES

6.1 ABSTRACT

Chimpanzee introductions are difficult events to manage and with little empirical evidence exploring the process, systematic models to predict outcomes are mostly nonexistent. The purpose of this study was to assess the predictive power of three measurements (visual access period, personality profiles, and video introductions) on the behavioural outcomes of the introductions. Social behaviours during the visual access period; the Hominoid Personality Questionnaire (Weiss et al., 2009); and social behaviours, SDBs, and time spent watching the video introductions, were compared against estimated percentages of time spent exhibiting aggressive, affiliative, and neutral behaviours towards others. Personality profiles had the most predictive power, whereas the video introductions had limited predictive power, and the visual access period had none. While keepers hosting the introductions are well-versed in the behaviour and personalities of their own chimpanzees, cross-institutional transfers, by definition, include unfamiliar individuals. The use of low-cost and relatively quick quantifiable measures, particularly simplified versions of personality assessments, to help guide the introduction process is recommended.

6.2 INTRODUCTION

6.2.1 CHIMPANZEE INTRODUCTIONS

Chimpanzees in the wild dynamically interact with different individuals within their own communities (Kummer, 1971; Aureli et al., 2008), but when faced with outside individuals or groups, interactions are often aggressive in nature (Wilson & Wrangham, 2003), regardless of each individuals' rank (Wilson et al., 2001). Permanently migrating from one group to another, generally by females when they become sexually mature (Nishida et al., 2003), is a challenging process. To become part of another group's social dynamic is not easy, as coalitions between females tend to be stable over time and males frequently change coalitions in order to increase their rank (de Waal, 1984).

Captive chimpanzee introductions have the potential, much like intergroup interactions in the wild, to be volatile; they are difficult and complex events to manage (Brent et al., 1997) and further research is

required to refine introduction methods and improve welfare. While moving primates between institutions to form new groups is a widespread practice in zoos and laboratories, introducing unfamiliar conspecifics can still be both psychologically and physically harmful (Joint Working Group on Refinement, 2009). The literature covering chimpanzee introductions is sparse with few published papers (i.e. van Hooff, 1973; Noon, 1991; McDonald, 1994; Brent et al., 1997; Fritz & Howell, 2001; Seres et al., 2001) and there is little empirical evidence exploring the behavioural predictors of introduction outcomes (Brent et al., 1997), particularly for high-risk mergers of larger groups mainly comprised of adults, which could potentially result in substantial injuries or worst-case scenarios: permanently isolating individuals from social groups or death (van Hooff 1973).

6.2.1.1 NATURALISTIC GROUPS

Naturalistic groups, as defined by Seres et al. (2001) include at least 15 apes consisting of multiple adult males and multiple adult females with offspring. Keeping chimpanzees in naturalistic groups in captivity is important as it is clear that it is necessary to help individuals to learn species appropriate behaviours and provides opportunities to build relationships and make choices within a socially dynamic environment (Noon, 1991; as reviewed by McDonald, 1994; Brent et al., 1997). The formation of larger, naturalistic groups, however, is not as prevalent as smaller groups, as many organisations do not have the facilities to support large, dynamic groups.

6.2.1.2 INTRODUCTION PROCESS AND USE OF VISUAL ACCESS

Introducing unfamiliar individuals to each other can be a stressful and challenging process for chimpanzees (Brent et al., 1997; Seres et al., 2001) and keepers. In contrast to the experience of a previously reported group formation where 18 individuals (5 males; 13 females) were sedated and released at the same time (van Hooff, 1973), most chimpanzee introductions now generally occur in several gradual steps where individuals can start to learn about each other and ease into the introduction process. According to game theory approaches, a calculation of success is based upon the choices of others (Maynard Smith, 1982); each individual's behaviour is determined by the behaviour of the other individuals in the group. A cost-benefit calculation estimating the likelihood of a successful outcome determines whether or not fighting is the best option (Matsumura & Okamoto, 2000;

Preuschoft & van Schaik, 2000); gradual introductions might provide the opportunity for chimpanzees to assess their competitors.

The introduction process generally starts by providing visual access before proceeding to physical introductions (often in dyads), and ultimately separating these newly introduced individuals to create a new group (Fritz & Fritz, 1979; Noon, 1991; McDonald, 1994; Alford et al., 1995; Brent et al., 1997; Seres et al., 2001; Fritz & Howell, 2001). The process does not end once individuals are housed together in groups; dependent upon the personality and priorities of the individuals involved, the battle for dominance might take a considerable amount of time, and as a hierarchy develops, the individuals involved must constantly prove themselves to stay in high-ranking positions (de Waal, 1982). Despite all of the efforts of staff and chimpanzees, however, group cohesion can never be guaranteed (Seres et al., 2001).

Conducting chimpanzee introductions is an art just as much as it is a science. We might expect sex or rank differences because males are known to exhibit more aggression than females (Alford et al., 1995; Brent et al., 1997; Muller, 2002) and high-ranking individuals exhibit more aggression than low-ranking individuals (Muller & Wrangham, 2004), but many factors about each individual involved are in play. The dynamics of each pair or group being introduced contains an element of the unknown. To minimise risk, the animal management team used an individualised management approach (Seres et al., 2001) where welfare was prioritised and individual wellbeing was considered throughout this large-scale chimpanzee introduction (i.e. qualitative accounts of each individual's personality, social tendencies, and needs were taken into consideration).

6.2.1.3 CONFLICTING REVIEWS

Gradual introductions, which provide the opportunity for chimpanzees to gain experience with each other in a protected and controlled environment, have received conflicting reviews. Familiarity has been noted to be an important factor in reducing aggressive interactions between chimpanzees (Fritz & Fritz, 1979), but research has also shown that prior exposure is not always required for an introduction to be successful (Brent et al., 1997). In a variety of monkeys, Bernstein (1991 as cited in Brent et al., 1997) suggested that while there is no evidence to support gradual over direct introductions, a visual access,

non-contact period could potentially predict compatibility. More recently, however, social behaviours have been seen to change over time when gradually building up to physical contact in chimpanzee introductions (Bloomsmith et al., 1998); compared to baseline levels, agonism increased during the visual access period and did not further increase during the physical introductions, whereas passive behaviours did the opposite and decreased during visual access and increased during physical introductions.

6.2.2 PERSONALITY IN NON-HUMAN PRIMATES

6.2.2.1 RATING SCALES

Individual differences and personality in non-human primates has been a topic of research for many decades (e.g. Crawford, 1938; Yerkes, 1939; Hebb, 1946; Goodall, 1971; Chamove et al., 1972; Buirski et al., 1978; Stevenson-Hinde & Zunz, 1978; Gold & Maple, 1994; King & Figueredo, 1997; Gosling, 2001; Weiss et al., 2009). Empirical studies initially focused on behavioural assessments including emotions (Chamove et al., 1972) with rating scales using traits emerging in the 1990s (Stevenson-Hinde & Hinde, 2011). The Five Factor Model (FFM), also known as the Big Five (Goldberg, 1990): Extraversion, Conscientiousness, Agreeableness, Neuroticism, and Openness, has been used in human personality profiles to successfully predict outcomes of group performance in business settings. Ideal groups included a combination of individuals with a mixture of high and low scores on Extraversion and Neuroticism and at least a few individuals with high scores on Conscientiousness, Agreeableness, and Openness (Neuman et al., 1999). Based on the FFM, human personality studies served as the starting point to assess personality in non-human primates (Gold & Maple, 1994; King & Figueredo, 1997).

King and Figueredo (1997) were the first to assess the FFM and relate the factors to chimpanzees, where a sixth factor was discovered: Dominance. Their original 43-adjective questionnaire was later referred to as the Hominoid Personality Questionnaire which included a total of 54 adjectives (Weiss et al., 2009) with ensured validity across different habitats and rater nationalities (King et al., 2005; Weiss et al., 2007; Weiss et al., 2009). To ensure a uniform understanding by raters of each term in relation to non-human primate behaviour, each adjective was followed by a few sentences describing the term (see Appendix B8).

6.2.2.2 APPLIED USE

When you talk to any keeper about their animals, personality or individual differences are inevitably mentioned. While evidence-based, animal management is able to incorporate the subjective opinions of those who work closely with the animals. By asking staff to complete personality assessments for individual animals, researchers are able to quantify the subjective opinions of those who know the animals best and test the results against patterns of behaviour in order to predict future behaviour (King & Weiss, 2011).

Although it would be ideal to use personality ratings as a low-cost and less labour-intensive method of making informed management decisions, in combination with each animal's unique history, literature pertaining to using these assessments in management situations is limited (e.g. Kuhar et al., 2006). Critics of the subjective rating method suggest that behavioural coding provides more reliable assessments than subjective ratings (Uher & Asendorpf, 2008). For a succinct review of the pros and cons for each method, see Freeman et al. (2011). While more research is certainly needed to fully assess the applicability of assessments to behavioural patterns, relationships between traits and behaviour have been found in chimpanzees (Pederson et al., 2005) and gorillas (Kuhar et al., 2006). Research is also underway to identify the stability of personality ratings over time with different raters and environmental conditions (Weiss et al., in prep).

6.2.3 USE OF VIDEO

Video technology has been successfully used in research and as enrichment with a number of chimpanzee groups (Menzel et al., 1985; Bloomsmith et al., 1990 & 2000; Bloomsmith & Lambeth, 2000; Hirata, 2007; see Chapter 4) and has informally been used as "video dating" for Koko the gorilla (P. Patterson, personal communication, 2006). Despite interest in the technology from researchers, keepers, and chimpanzees, video has not yet been tested as a potential tool to enhance animal management in the creation of new groups.

For the past 18 months, we have studied chimpanzee responses to different video content (including live feeds of familiar conspecifics and locations) and recorded self-directed behaviours (SDBs) to monitor arousal in response to our training methods (see Chapter 3) as each individual differs in how

they express internal states (Yamanashi & Matsuzawa, 2010). We found no negative impact of training but were also interested in the possibility that this training might be used to positively enhance welfare as a stage in assessing individuals prior to and during the introduction process.

6.2.4 STUDY AIMS

This study aimed to examine a large-scale chimpanzee introduction. Since introductions of this nature are unusual events, the observations and analyses in this chapter will help fill the gap in the literature. A primary, yet challenging goal in introductions is to be able to gauge cues (vocal and non-vocal) from the chimpanzees and react appropriately to provide a suitable environment in which they can develop dynamic social groups (Seres, 2008). With each chimpanzee introduction having the potential to be different, having models to gauge the likelihood of success with specific combinations would be beneficial. We studied three methodological categories to determine predictability of introduction outcomes that might help reduce risk and lead to improvements in welfare by guiding future introductions (e.g. highlighting likely aggressive, affiliative, or neutral combinations based on statistical models). Of particular interest were visual access (an early phase of the introduction where chimpanzees could see, but not touch each other), personality profiles, and video introductions. These concepts were explored in five analytical categories in which we identified seven questions and hypotheses:

ANALYSIS 1: VISUAL ACCESS

How often did the chimpanzees exhibit aggressive, affiliative, neutral, or avoiding social behaviours during the visual access period?

ANALYSIS 2: PERSONALITY PROFILES

What were the chimpanzees' personality profiles?

ANALYSIS 3: VIDEO INTRODUCTIONS

What percentage of time did the chimpanzees watch the video introductions and how often did they exhibit SDBs and social behaviours?

ANALYSIS 4: PHYSICAL INTRODUCTIONS

How often did the chimpanzees exhibit aggressive, affiliative, neutral, or avoiding social behaviours during the physical introductions?

ANALYSIS 5: PREDICTORS OF INTRODUCTION OUTCOMES

When considering the different sex and rank interactions possible during the introductions (see Appendix G2):

(a) Can the social behaviours observed during the visual access period (an early phase within the introductions) be used to predict behaviours during physical introductions?

(b) Can personality profiles be used to predict behaviours during physical introductions?

(c) Can the SDBs, social behaviours observed and time spent watching the video introductions be used to predict behaviours during physical introductions?

6.3 METHODS

6.3.1 STUDY ANIMALS

The study animals were two groups of 11 chimpanzees (*Pan troglodytes*) each. Both groups (Edinburgh and Beekse Bergen) were of similar size, sex composition, and age ranges with the Edinburgh group including slightly older individuals. At the onset of the study, March 2010, the Edinburgh group included 5 males and 6 females ranging in age from 11 to 49 years old (mean = 27.73, SE mean = 3.76); the Beekse Bergen group included 6 males and 5 females ranging in age from 13 to 41 years old (mean = 21.64, SE mean = 2.48). Additional information on the group, their management, and housing conditions is described in Chapter 2, General Methods.

6.3.2 APPARATUS

In addition to software mentioned in Chapter 2, General Methods, paper checksheets (see Appendices B4 – B6), along with a beeper for point sampling were used. Two cameras (Sanyo Xacti HD700 and Panasonic SDR-8W21) were used to record footage of chimpanzees to be shown during the video introductions. Two computers (Apple MacBook MB062LL/B and Toshiba Satellite Pro U400) were used

to edit the videos with QuickTime Pro. The MacBook was also used to play the videos for the chimpanzees to view on a 19" open-frame flat screen computer monitor (Elo 1939L) that was mounted on a steel L-shaped cart with 12mm sheet of Perspex in front of the monitor to protect it from the chimpanzees (e.g. jabbing with sticks or spitting).

6.3.3 RESEARCH DESIGN

6.3.3.1 PHYSICAL INTRODUCTION

Physical introductions were held on a goal oriented, yet flexible schedule with the aim to merge the two groups into one as soon as possible, provided the chimpanzees' welfare was maintained at an acceptable level as determined by keeper evaluation. There were three main stages during the introductions: auditory access, visual access, and physical introductions. Each new stage began only when the keepers felt the chimpanzees had reasonably habituated to the previous stage as evidenced by increased neutral behaviours and a decrease in aggressive behaviours.

Upon the new chimpanzees' arrival, both groups were housed in separate areas of the enclosure where visual access was blocked (i.e. the centre bed of the off-exhibit area, see Figure 2.4C, was filled with bales of straw), however, the groups could hear and smell each other. After six days, visual access was provided with a two-metre wide barrier including two layers of steel mesh between them (i.e. the centre bed). After one week, when the chimpanzees gained experience meeting each other from a distance, the physical introductions began. Preliminary physical introductions included a mix of visual access and a few select introduction dyads and small groups in order to assess pairing suitability before the creation of the new group of chimpanzees, called the "super group". The "super group" included members from the Beekse Bergen and Edinburgh groups who had been successfully introduced.

The physical introductions always started off with two or more individuals meeting through two layers of steel mesh (i.e. one bed enclosure between them). At the keepers discretion (e.g. when they felt the introduction would likely continue in a positive direction), one slide was opened allowing the chimpanzees to interact via protected contact where one layer of steel mesh was between them. At this point they could touch each other through the mesh. Upon keeper approval of the behaviours exhibited from both parties (e.g. affiliative, submissive, or neutral), the slide between the individuals was opened

and the chimpanzees could physically interact without any barriers. If the chimpanzees were exhibiting aggressive behaviours, the protective contact phase either continued in the hopes that aggression would subside, or introductions were aborted. If all went well with the physical contact introductions, the individuals were moved into an area dedicated to the new group (i.e. the “super group”). If the “super group” had already started, prior to being moved into the new group’s room, the “super group” individuals were brought into the introduction area so all could meet in a controlled environment before officially becoming a part of the “super group”.

If, at any stage in the process, the introductions did not go well, the keepers safely separated the chimpanzees and reassessed combinations. A few dyads and small groups needed introduction durations of more than one day to get to know each other, during which cases, the keepers separated those involved in the introduction within the off-exhibit area from their original groups until the introduction was over. A timeline of the introductions can be seen in Appendix H. The entire introduction process, including two breaks for medical or logistic purposes, took just over 3.5 months.

6.3.3.2 PERSONALITY ASSESSMENT

Personality profiles were assessed using the Hominoid Personality Questionnaire (see Appendix B6), an established method of personality assessment in chimpanzees (King & Figueredo, 1997; Weiss et al., 2009).

6.3.3.3 VIDEO INTRODUCTIONS

Several video clips lasting five minutes each were recorded prior to the Beekse Bergen chimpanzees’ arrival in Edinburgh. Both groups were filmed in their original enclosures (i.e. the Edinburgh group in Budongo Trail and the Beekse Bergen group in Safaripark Beekse Bergen) showing activity both inside and outside enclosures. As this was the first video study in conjunction with introductions, neither the researcher nor keeping staff could predict the reaction from the chimpanzees. In order to avoid causing any unnecessary aggression, the content of the videos was controlled to show generally calm situations (e.g. foraging, resting, locomoting, grooming, etc.).

Sessions were held as frequently as possible throughout the introduction process so at least one session was held during each stage (i.e. auditory access, visual access, preliminary introductions, and “super group” introductions). Eleven pairs of video introduction sessions were interwoven with the physical introduction process (see Appendix H). A pair of sessions included up to one hour of video clips for each group with a total of 9 hours and 20 minutes presented to each group overall. To avoid new stages in the introduction process occurring before a pair of sessions could be complete, the groups were presented with the footage separately, where one group’s session occurred in the afternoon and the other group’s session occurred the following morning.

Each time a new session occurred, the content within the one-hour stream of video (five-minute clips for each chimpanzee and one for the entire group) rotated to counterbalance the chimpanzee viewing order. As the group progressed into the phase of the introduction process where individuals were being removed to create the “super group”, the one-hour stream of video changed to show new five-minute clips of the new members in the “super group”. This not only permitted the habituation to unfamiliar individuals, but also to potentially monitor fission fusion during the development of a new group with some familiar individuals. Once the group reached 12 members, the length of each chimpanzee’s video clips was reduced to 2.5 minutes, to ensure the video sessions did not last longer than one hour.

During the video introduction sessions, the keepers maintained their usual cleaning routine, which included passing by the off-exhibit area. No extra efforts were made to interact with the chimpanzees when the videos were playing and no food reinforcement was provided for this study, however, food might have been left over in the area from a previous feed.

6.3.4 DATA COLLECTION

6.3.4.1 VISUAL ACCESS AND PHYSICAL INTRODUCTIONS

Observations of the introduction outcome were made after each physical introduction by the researcher and keeping staff. In addition to the overall success and failure (i.e. aborted) of each introduction, outcomes were defined by the social behaviours: aggressive, affiliative, neutral, and presence (see Table 2.5 for definitions) exhibited by each chimpanzee involved. Submissive behaviours were also noted, but omitted from analyses due to low IOR. Using a paper check sheet (see Appendix

B6), the percentage of time spent exhibiting social behaviours was estimated for all possible pairings on an individual basis. For example, an introduction between Louis, Pearl, David, and Heleen included 12 sets of scores (e.g. Louis' behaviour towards the others involved in the introduction was separated into dyad-based scores: Louis to Pearl, Louis to David, and Louis to Heleen). The number of sets of scores observed per introduction can be expressed by the following equation: $n^2 - n$.

Observers, who had worked with chimpanzees for at least two years, were instructed to provide an estimated percentage of time spent engaged in each of the behavioural categories for all possible dyads within each introduction, based on their subjective, expert opinion of chimpanzee behaviour. They were also advised to omit ratings if they felt they could not accurately assess a particular dyad. Ratings were relied upon in lieu of behaviours due to the dynamic and complex nature of each introduction. The keepers' subjective opinion of behaviour was also the measure used by the animal management team to assess the introductions. Recording the individual behaviours for those involved in each introduction would have lead to unreliable results. Video footage was taken of each introduction, but was unsuitable to accurately assess overall behaviours due to limitations in the width of the area being filmed and in the ability to identify individuals and behaviours through two layers of mesh.

6.3.4.2 PERSONALITY ASSESSMENT

Hominoid Personality Questionnaires (see Appendix B6) were completed by five keepers and the primary researcher (Edinburgh: $n = 4$ and Beekse Bergen: $n = 2$), who were familiar with the chimpanzees and had known them for at least two years. Personality traits were assessed with information prior to the transport and relocation of the Beekse Bergen group to Edinburgh Zoo (i.e. up to 17 March 2010) and formulated scores for six personality factors (see Table 2.5).

6.3.4.3 VIDEO INTRODUCTIONS

Data were recorded in real-time as chimpanzees watched the video introductions. Behaviour sampling was used in the continuous recording of SDBs and social behaviours for all individuals and instantaneous time sampling (Martin & Bateson, 2007) in 30-second increments was used to record the location of each individual (i.e. present or not) and whether or not they were watching the video (see Table 6.1).

Table 6.1. Predictors, outcomes, and measurements used for each category in backward stepwise regressions for the behaviours exhibited during chimpanzee introductions.

Type	Predictor	Visual Access	Video Intros	Personality Profiles	Outcome
Social behaviours	Aggressive	Estimated %	All occurrences		Estimated %
	Affiliative	Estimated %	All occurrences		Estimated %
	Neutral*	Estimated %			Estimated %
	Not Present*	Estimated %			
Self-directed behaviours	Scratch		All occurrences		
	Rub		All occurrences		
	Self Groom		All occurrences		
	Yawn		All occurrences		
Watch	Watch		Estimated %		
Personality factors	Dominance			Avg rating	
	Extraversion			Avg rating	
	Conscientiousness			Avg rating	
	Agreeableness			Avg rating	
	Neuroticism			Avg rating	
	Openness			Avg rating	

Note: An asterisk (*) indicates social behaviours (neutral and not present) that were not used for the video introduction analysis because the behavioural measure of rate/minute was only suited to proactive behaviours.

6.3.5 DATA ANALYSIS

6.3.5.1 EVENT AND STATE BEHAVIOURS

Rates per minute were calculated by dividing event frequency, the number of data points, by the duration of the observation sessions (during which the focal animals were always in view). Estimated percentage of time spent exhibiting a behaviour was calculated by dividing the number of point samples (raw score) of each behaviour by the total number of sample points (Martin & Bateson, 2007). Rates per minute (for events: SDBs) and estimated percentages (for states: social behaviours and watching) were used to allow for comparisons across all categories, with each individual contributing one mean rate per phase or condition to avoid pseudo-replication of data (Dawkins, 2007). SDB data were reported by individual behaviour instead of one category of SDB because the behaviours did not follow the same patterns in these analyses (Chapter 3 included data analyses on a unified category of SDBs because the individual behaviours were exhibited in similar patterns).

6.3.5.2 PERSONALITY ASSESSMENT

Following Weiss et al. (2009), variable scores from each rater were unit-weighted and listed as positive or negative in accordance with the defined loadings for each personality factor (see Table 2.5). After omitting the variables that did not have acceptable levels of IOR (see Section 6.3.6.4), the remaining scores were averaged together to create six factor scores for each chimpanzee/rater combination. Each chimpanzee's scores (from n raters) were then averaged to create six personality factor scores for each chimpanzee. Unit-weighted factor scores were converted into T-scores to simplify interpretation (King et al., 2005; Weiss et al., 2007 & 2009).

6.3.5.3 REGRESSIONS

The effects of three categories (visual access, video introductions, and personality) were assessed using multiple linear regressions in which all data points (with one averaged datum point per individual) were used. Each category examined five different sampling combinations in order to detail behavioural differences for all individuals, then separated by sex (males and females), and by rank (high and low ranks). These combinations were compared against each other and the social context (in- and out-groups) for three behavioural outcomes: aggressive, affiliative, and neutral (see Appendix G1 for a matrix of the analyses for each category). A total of 21 multiple regressions were performed for each of the five sampling combinations within the three categories. The results highlight only those regression analyses that produced significant models. Significance was set at 0.05 with follow-up analyses (where samples were split by sex or rank) set at $p < 0.025$ (see Appendix G1).

The video introduction analyses differed slightly in that each regression combination (see Appendix G1) was in relation to individuals in the sampling combination watching videos that matched the outcome variable (e.g. females watching females and how those behaviours predicted how they would behave towards females during introductions, or females watching males and how those behaviours predicted how they would behave towards males during introductions).

Backward stepwise linear regressions were used to examine the best-fit model of predictor variables (Field, 2009). Different predictors were used based upon the category being assessed (see Table 6.1 for a list of predictors and Table 2.5 for their behavioural definitions). With five data points recommended

per predictor (Allison, 1999), the sample size of 22 individuals could support up to four predictors in a given model. Even though more than four variables were entered into each regression, this did not affect the overall degrees of freedom for significant models with four or fewer predictors, because identical outputs were reached from (a) a regression with six variables producing two significant predictors compared to (b) a regression with only the two significant predictors listed as variables. Subsequent analyses where the individuals were separated by sex and rank decreased the number of predictors in accordance with the total sample size. Significant models with too many predictors were omitted due insufficient degrees of freedom. Statistically speaking, a sample size of 22 individuals is considered small; however, given that the introductions observed for this study were the largest to take place in the literature, from an applied perspective, the sample size was considered large.

Outliers were not omitted from the analyses as all participants were deemed biologically relevant and important to include. Regression combinations were omitted if they did not meet the statistical assumptions (Field, 2009): variable types must be quantitative or categorical, variance across predictors cannot be zero, no perfect multicollinearity among predictors, no correlations with external variables, homoscedasticity among residuals, no autocorrelation, normally distributed errors, outcome variables are independent, and the model relationship is linear.

Multicollinearity was assessed through the variance inflation factor (VIF) and tolerance scores and through a correlation matrix of potential predictors where any highly correlated ($r > 0.900$) variables were omitted from the analyses. To avoid autocorrelation within the data, any significant models with Durbin-Watson scores less than 1.000 or more than 3.000 were omitted. Models with histograms and normal probability plots indicating non-normality were omitted, as were any models with residual plots indicating heteroscedasticity and non-linearity. Significant statistics including adjusted R^2 (ΔR^2) values are presented in the results section, with a larger matrix visualising all tested pairs and significant models in the Appendix (see Appendix G1).

6.3.5.4 INTER-OBSERVER RELIABILITY

Inter-observer (or inter-rater) reliability (IOR) was tested between all observers rating physical introductions and personality traits (see Section 6.3.6.2). IOR was calculated using Intraclass Correlation

Coefficients (ICC), as this test is suitable for multiple raters (Shrout & Fleiss, 1979). For the personality ratings, a total of 44 variables were included in the analyses due to acceptable rates of reliability (see Appendix G2-A) as those with ICC scores at or below zero were omitted (Weiss et al., 2011). For the introduction ratings, data collected for IOR testing occurred for a five minute interval during which all social behaviour categories were observed. ICC statistics were used to assess four raters (the researcher and three keepers) where one category, submissive behaviour, was omitted due to low reliability across observers (see Appendix G2-B). An additional observer recorded data for IOR during the physical introductions along side the researcher. Although all behaviours were observed, there were not enough data points (e.g. only two chimpanzees were observed) to permit a correlation to be calculated. Since the observer's data nearly equaled those of the researcher (who was also included in the ICC), the additional observer's data were included in the analyses.

6.4 RESULTS

6.4.1 ANALYSIS 1: VISUAL ACCESS

During the visual access period, the chimpanzees spent the majority of their time avoiding the introduction area (i.e. not present) by remaining in adjoining enclosure areas (mean = 42.768%, SE mean = 5.482%). This was followed by the estimated percentage of time they spent exhibiting neutral behaviours (mean = 27.738%, SE mean = 4.788%), aggressive behaviours (mean = 24.623%, SE mean = 5.930%), and affiliative behaviours (mean = 3.871%, SE mean = 1.472%) towards others (see Figure 6.1).

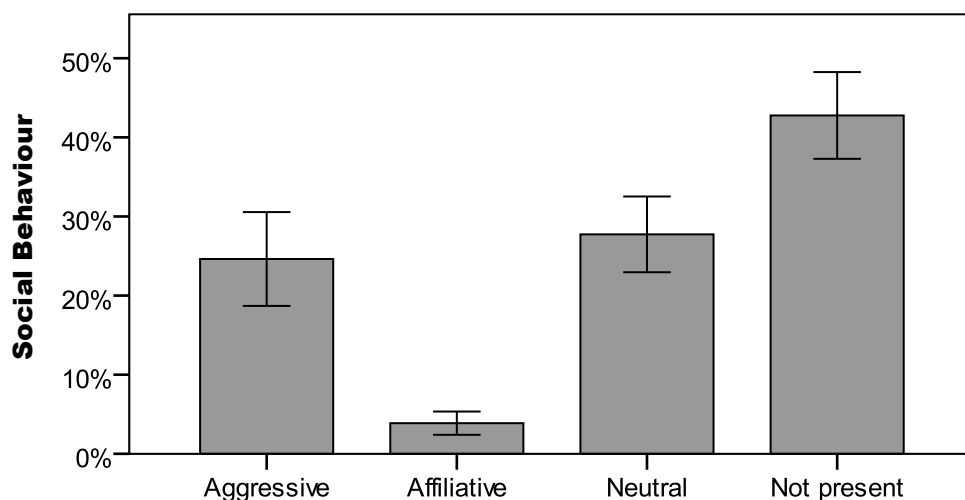


Figure 6.1. A comparison of the mean (\pm 1 SE) estimated percentage of time engaging in social behaviours (aggressive and affiliative) during the visual access period.

6.4.2 ANALYSIS 2: PERSONALITY PROFILES

The chimpanzees' personality profiles varied across individuals (see Table 6.3 and Figure 6.2). With a standardised mean of 50 (and SD = 10) for each factor, the range spanned two to three standard deviations in each direction: Dominance (27.50 – 64.75), Extraversion (31.72 – 67.22), Conscientiousness (30.16 – 65.89), Agreeableness (24.96 – 65.29), Neuroticism (36.80 – 74.80), and Openness (32.21 – 63.89).

Table 6.3. Personality profiles described as six factors with T scores for each chimpanzee based on the Hominoid Personality Questionnaire.

	Dominance	Extraversion	Conscientiousness	Agreeableness	Neuroticism	Openness
Bram	51.81	28.67	53.71	38.66	41.02	31.04
Cindy	43.44	38.31	67.52	59.96	49.94	68.00
Claus	62.66	47.95	35.03	24.96	48.53	46.29
David	50.86	47.95	52.49	56.16	44.77	47.47
Edith	49.28	50.99	43.96	38.66	56.04	54.51
Emma	61.59	58.09	59.80	62.24	36.80	56.85
Eva	64.75	50.99	54.52	43.22	41.96	61.55
Frek	53.39	58.09	56.15	44.74	54.22	50.99
Heleen	37.29	37.80	32.59	44.74	65.42	40.43
Kilimi	45.81	44.90	61.43	50.07	40.55	53.92
Kindia	56.38	55.05	41.93	45.50	46.18	51.57
Lianne	27.50	31.72	44.78	56.92	74.80	33.39
Liberius	50.39	67.22	43.56	38.66	50.87	60.96
Louis	60.17	60.12	49.65	52.35	41.02	56.27
Lucy	50.07	43.89	51.68	49.31	49.00	49.81
Lyndsey	45.97	48.96	54.12	61.48	45.24	51.57
Paul	61.91	56.06	58.58	47.79	39.14	49.81
Pearl	54.65	58.09	65.89	56.92	41.96	54.51
Qafzeh	55.60	56.06	30.16	43.98	48.53	41.01
Rene	48.34	64.18	45.59	59.96	59.79	63.89
Ricky	35.39	42.88	52.09	65.29	57.91	32.21
Sophie	33.18	52.01	44.78	58.44	67.30	43.95

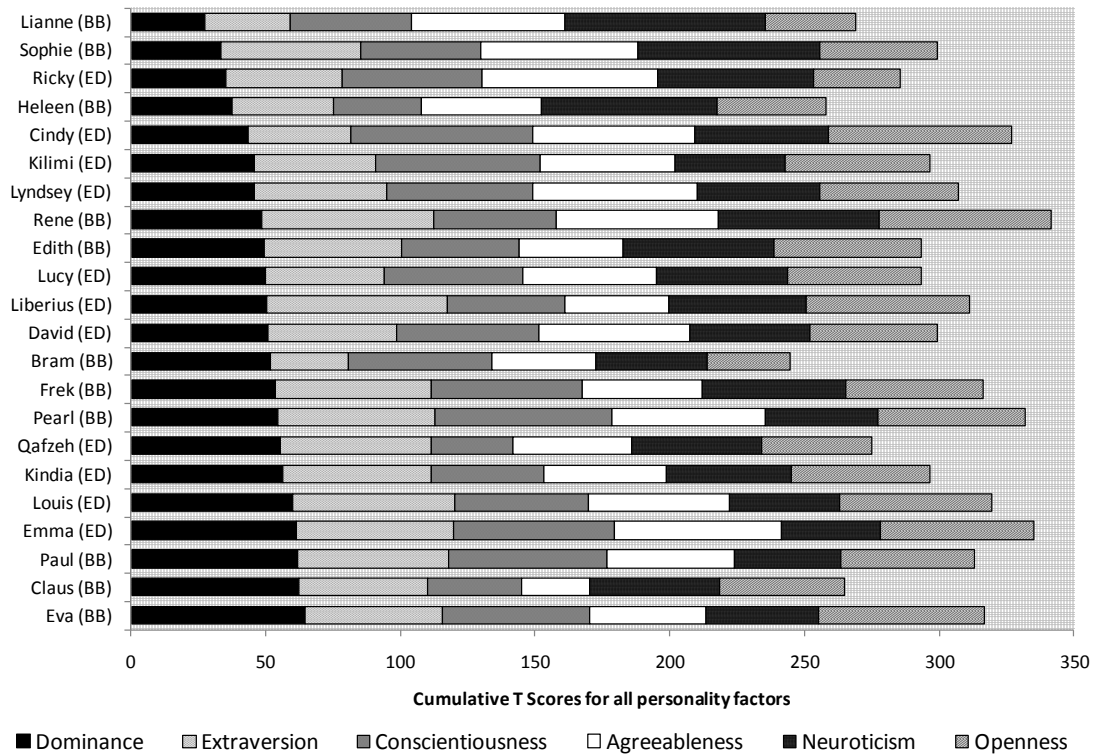


Figure 6.2. Personality profiles of the chimpanzees in order of the Dominance factor, from lowest to highest (top to bottom) with original group listed in parentheses. Different colours represent the T score for each chimpanzee's personality factors (as defined in the legend).

6.4.3 ANALYSIS 3: VIDEO INTRODUCTIONS

Of the 9 hours and 20 minutes of video introductions presented to each group, the chimpanzees watched an average of 12% of the time (mean = 12.04%, SE mean 1.45%). Rates per minute for SDBs and social behaviours were fairly infrequent: scratching (mean = 0.06, SE mean = 0.01), rubbing (mean = 0.01, SE mean = 0.002), self grooming (mean = 0.02, SE mean = 0.004), yawning (mean = 0.01, SE mean = 0.002), and exhibiting aggressive (mean = 0.01, SE mean = 0.002) and affiliative behaviours (mean = 0.01, SE mean = 0.002) towards other or the monitor (see Figure 6.3).

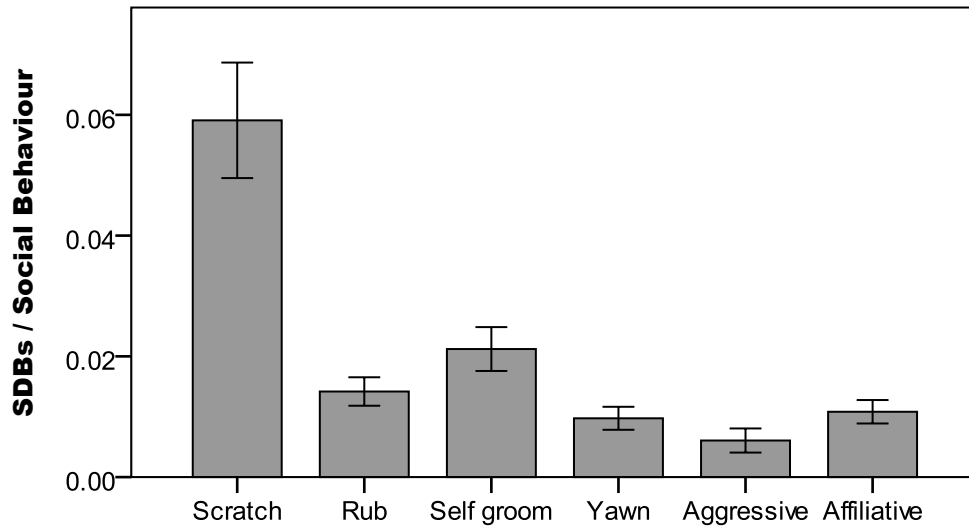


Figure 6.3. A comparison of the mean (\pm 1 SE) rate per minute for SDBs (scratch, rub, self groom, and yawn) and social behaviours (aggressive and affiliative) during the video introductions.

6.4.4 ANALYSIS 4: PHYSICAL INTRODUCTIONS

The chimpanzees exhibited neutral behaviours the most during the physical introductions (mean = 47.902%, SE mean = 2.448%), followed by avoiding the introduction area (i.e. not present), which was only possible during the visual access days that were interwoven throughout the dyad and small group introductions (mean = 22.605%, SE mean = 2.538%), followed by exhibiting affiliative behaviours (mean = 11.124%, SE mean = 1.375%), and aggressive behaviours (mean = 9.783%, SE mean = 1.449%) towards others (see Figure 6.4).

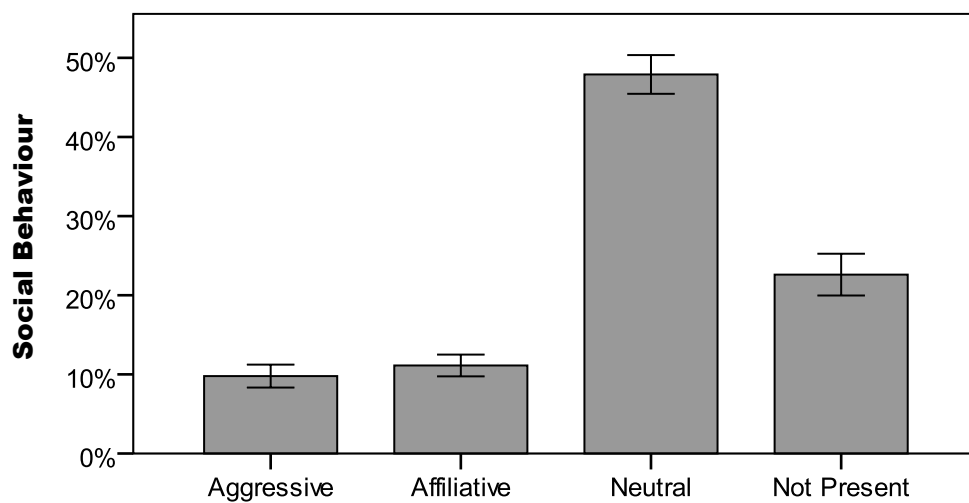


Figure 6.4. A comparison of the mean (\pm 1 SE) estimated percentage of time engaging in social behaviours (aggressive, affiliative, neutral, and not present) during the physical introductions.

6.4.5 ANALYSIS 5: PREDICTORS OF INTRODUCTION OUTCOMES

6.4.5.1 VISUAL ACCESS

Predictor variables for social behaviours observed during the visual introductions (aggressive, affiliative, and neutral) were entered into the regression models to predict behaviours for 105 paired combinations that will be encountered during the physical introductions (see Appendix G). Surprisingly, none of the variables had an impact on the tested pairs and produced no significant models.

6.4.5.2 PERSONALITY PROFILES

Predictor variables for the six chimpanzee personality factors were entered into the regression models to predict behaviours all 105 paired combinations (see Appendix G1). Twelve models were significant (see Tables 6.4 – 6.6) where Conscientiousness seemed to be the most consistent across the models.

Aggressive behaviours were predicted by Dominance, Agreeableness, and Extraversion (see Table 5.4). Three models suggest that in predicting how certain individuals will behave towards others during the introductions: The higher the Dominance, the more aggressive all individuals will be to males, explaining a moderate proportion of variance (29.5%). The lower the Agreeableness the more aggressive all individuals will be to unfamiliar, out-group individuals (22.8%). The lower the Extraversion, the more aggressive low ranked individuals will be towards familiar, in-group individuals, reintroduced when the “super group” was in development (53.6%).

Table 6.4. Significant models predicting aggressive behaviours during the physical introductions based on personality factors.

Models	B	SE B	β	T	Sig
All individuals towards males	$\Delta R^2 = 0.295, F_{2,19} = 5.403, p = 0.014$				
<i>Constant</i>	-1.353	5.888		-0.230	0.821
<i>Dominance</i>	0.385	0.117	0.699	3.285	0.004
<i>Extraversion</i>	-0.209	0.117	-3.790	-1.779	0.091
All individuals towards out-group	$\Delta R^2 = 0.228, F_{1,20} = 7.200, p = 0.014$				
<i>Constant</i>	30.224	7.504		4.018	0.001
<i>Agreeableness</i>	-0.395	0.147	-0.514	-2.683	0.014
Low ranks towards in-group	$\Delta R^2 = 0.536, F_{1,6} = 9.097, p = 0.024$				
<i>Constant</i>	3.412	0.943		3.617	0.011
<i>Extraversion</i>	-0.065	0.021	-0.776	-3.016	0.024

Affiliative behaviours were predicted by Conscientiousness and Neuroticism (see Table 6.5). Three models suggest that in predicting how certain individuals will behave towards others during the introductions: The lower the Conscientiousness, the more affiliative all individuals will be to females, explaining a small percentage of the variance (13.7%) and the lower the Conscientiousness and Neuroticism, the more affiliative all individuals will be to low ranks (37.1%).

Table 6.5. Significant models predicting affiliative behaviours during the physical introductions based on personality factors.

Models	B	SE B	β	T	Sig
All individuals towards females	$\Delta R^2 = 0.137, F_{1,20} = 4.337, p = 0.050$				
<i>Constant</i>	45.990	13.530		3.399	0.003
<i>Conscientiousness</i>	-0.553	0.266	-0.422	-2.083	0.050
All individuals towards low ranks	$\Delta R^2 = 0.371, F_{3,16} = 4.741, p = 0.015$				
<i>Constant</i>	95.601	26.101		3.663	0.002
<i>Conscientiousness</i>	-1.453	0.398	-1.067	-3.655	0.002
<i>Agreeableness</i>	0.642	0.318	0.514	2.019	0.061
<i>Neuroticism</i>	-0.693	0.335	-0.555	-2.067	0.005

Neutral behaviours were predicted by Conscientiousness, Extraversion, and Neuroticism (see Table 6.6). Seven models suggest that in predicting how certain individuals will behave towards others during the introductions: The higher the Conscientiousness, the more neutral behaviours will be exhibited by all individuals towards males, explaining a moderate proportion of variance (39.7%), towards in-group individuals (33.3%), and for males towards females (55%). High Conscientiousness combined with low Extraversion predicts the neutral behaviours for all individuals towards females (43.6%) and for females towards low ranks (58%); whereas when it is combined with low Agreeableness, predicts neutral behaviours for all individuals towards low ranks. The lower the Neuroticism, the more neutral all individuals will be towards out-group individuals (25.3%).

Table 6.6. Significant models predicting neutral behaviours during the physical introductions based on personality factors.

Models	B	SE B	β	T	Sig
All individuals towards females	$\Delta R^2 = 0.436, F_{3,18} = 6.398, p = 0.004$				
Constant	49.039	13.709		3.577	0.002
Dominance	0.387	0.214	0.349	1.807	0.087
Extraversion	-0.546	0.213	-0.493	-2.569	0.019
Conscientiousness	0.568	0.184	0.513	3.082	0.006
All individuals to males	$\Delta R^2 = 0.397, F_{1,20} = 14.852, p = 0.001$				
Constant	9.623	12.949		0.743	0.466
Conscientiousness	0.980	0.254	0.653	3.854	0.001
All individuals to low ranks	$\Delta R^2 = 0.355, F_{2,17} = 6.221, p < 0.001$				
Constant	45.310	15.179		2.985	0.008
Conscientiousness	1.034	0.295	0.721	3.506	0.003
Agreeableness	-0.693	0.335	-0.555	-2.067	0.005
All individuals to in-group	$\Delta R^2 = 0.333, F_{1,20} = 11.484, p = 0.003$				
Constant	17.646	13.305		1.326	0.200
Conscientiousness	0.885	0.261	0.604	3.389	0.003
All individuals to out-group	$\Delta R^2 = 0.253, F_{2,19} = 4.559, p = 0.024$				
Constant	72.484	21.468		3.376	0.003
Agreeableness	0.629	0.322	0.371	1.952	0.066
Neuroticism	-0.819	0.322	-0.483	-2.541	0.020
Females to low ranks	$\Delta R^2 = 0.580, F_{2,7} = 7.203, p = 0.020$				
Constant	67.562	16.904		3.997	0.005
Extraversion	-0.0855	0.335	-0.579	-2.554	0.038
Conscientiousness	0.843	0.245	0.781	3.345	0.011
Males to females	$\Delta R^2 = 0.550, F_{2,8} = 7.111, p = 0.017$				
Constant	44.729	12.720		3.517	0.008
Conscientiousness	1.004	0.272	0.864	3.691	0.006
Agreeableness	-0.489	0.216	-0.530	-2.264	0.053

6.4.5.3 VIDEO INTRODUCTIONS

Seven predictor variables including SDBs, social behaviours, and watching were entered into the regression models to predict behaviours for all 105 paired combinations (see Appendix G1). Nine models were significant (see Tables 6.7 – 6.9) where the combination of significant predictor variables depended on the individuals included in the model.

Aggressive behaviours were predicted by the percentage of time spent watching and rates of scratching, yawning and exhibiting affiliative behaviours (see Table 6.7). Four significant models suggest that in predicting how certain individuals will behave towards others during the introductions: Comparing rates and percents of behaviour across all group members, when all individuals watched all of the videos, the less they scratched and exhibited affiliative behaviours while yawning more, the more aggressive they would behave towards all individuals, explaining a moderate percentage of the variance (42.2%). When all individuals watched videos of males, the more they watched and the more they yawned, the more aggressive they would behave towards males (33.6%). When males watched videos of males, the more they watched, the more aggressive they would behave towards males (43.2%). When all individuals watched videos of in-group (members of their own group who moved into the “super group”), the more they watched and the less they exhibited affiliative behaviours, the more aggressive they would behave towards all individuals (48.8%).

Table 6.7. Significant models predicting aggressive behaviours during the physical introductions based on the behaviours exhibited while watching videos of those in the category they are introduced to in the model.

Models	B	SE B	β	T	Sig
All individuals towards all	$\Delta R^2 = 0.422, F_{3,18} = 6.112, p = 0.005$				
Constant	15.828	2.257		7.014	< 0.001
Scratch	-78.152	25.448	-0.516	-3.071	0.007
Yawn	323.886	148.642	0.426	2.179	0.043
Affiliative	-423.335	144.641	-0.567	-2.927	0.009
All individuals towards males	$\Delta R^2 = 0.336, F_{2,19} = 6.323, p = 0.008$				
Constant	2.230	1.814		1.229	0.234
Yawn	96.768	41.523	0.414	2.330	0.031
Watch	0.190	0.069	0.491	2.759	0.012
All individuals towards in-group	$\Delta R^2 = 0.488, F_{2,12} = 7.671, p = 0.007$				
Constant	1.213	0.435		2.789	0.016
Affiliative	-38.404	15.099	-0.488	-2.543	0.026
Watch	0.045	0.016	0.533	2.779	0.017
Males towards males	$\Delta R^2 = 0.432, F_{1,9} = 8.599, p = 0.017$				
Constant	4.590	2.237		2.052	0.070
Watch	0.267	0.091	0.699	2.932	0.017

Affiliative behaviours were predicted by the percentage of time spent watching and rates of scratching and self grooming (see Table 6.8). Two significant models suggest that in predicting how certain individuals will behave towards others during the introductions: When all individuals watched all of the videos, the more they watched and scratched, the more affiliative they would behave towards all individuals, explaining a moderate percentage of the variance (28.8%). When high-ranked individuals watched video footage of other high-ranked individuals, the more they self groomed, the more affiliative they would behave towards other high-ranked individuals (55.9%).

Table 6.8. Significant models predicting affiliative behaviours during the physical introductions based on the behaviours exhibited while watching videos of those in the category they are introduced to in the model.

Models	B	SE B	β	T	Sig
All individuals towards all	$\Delta R^2 = 0.288, F_{4,17} = 3.127, p = 0.042$				
<i>Constant</i>	4.439	2.683		1.655	0.116
<i>Scratch</i>	81.034	33.109	0.564	2.447	0.026
<i>Rub</i>	-329.502	157.497	-0.565	-2.092	0.052
<i>Aggressive</i>	-341.469	196.223	-0.496	-1.740	0.100
<i>Watch</i>	0.699	0.281	0.759	2.483	0.024
High ranks towards high ranks	$\Delta R^2 = 0.559, F_{1,6} = 9.865, p = 0.020$				
<i>Constant</i>	11.618	2.110		5.507	0.002
<i>Self groom</i>	94.693	30.148	0.789	3.141	0.020

Neutral behaviours were predicted by the percentage of time spent watching videos and rates of self grooming and exhibiting aggressive and affiliative behaviours (see Table 6.9). Three significant models suggest that in predicting how certain individuals will behave towards others during the introductions: When all individuals watched all of the videos, the more they self groomed, the more neutral they would behave towards all individuals, explaining a moderate percentage of the variance (41.3%). When males watched videos of females, the more they watched and exhibited aggressive behaviours, the more neutral they would behave towards females (76.4%). When all individuals watched videos of low-ranked individuals, the less they scratched while exhibiting more affiliative and aggressive behaviours, the more neutral they would behave towards low-ranked individuals (47.4%).

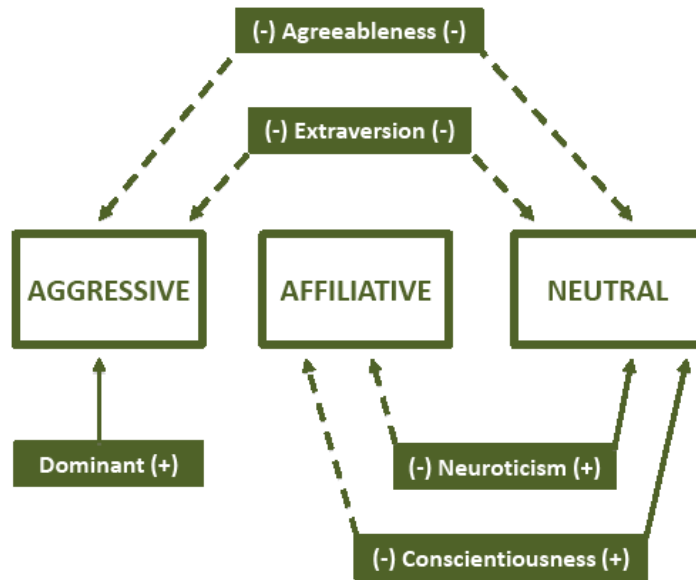
Table 6.9. Significant models predicting neutral behaviours during the physical introductions based on the behaviours exhibited while watching videos of those in the category they are introduced to in the model.

Models	B	SE B	β	T	Sig
All individuals towards all	$\Delta R^2 = 0.413, F_{2,19} = 8.388, p = 0.002$				
Constant	35.482	3.606		9.840	<0.001
Rub	355.687	178.840	0.343	1.989	0.061
Self groom	347.775	116.044	0.516	2.997	0.007
All individuals towards low ranks	$\Delta R^2 = 0.474, F_{3,16} = 6.708, p = 0.004$				
Constant	72.048	3.307		21.786	<0.001
Self groom	-100.272	43.018	-0.399	-2.331	0.033
Aggressive	71.523	33.331	0.367	2.146	0.048
Affiliative	324.277	122.429	0.466	2.649	0.018
Males towards females	$\Delta R^2 = 0.764, F_{2,8} = 17.150, p = 0.001$				
Constant	54.405	3.053		17.819	<0.001
Aggressive	381.045	124.338	0.471	3.065	0.015
Watch	0.659	0.131	0.771	5.013	0.001

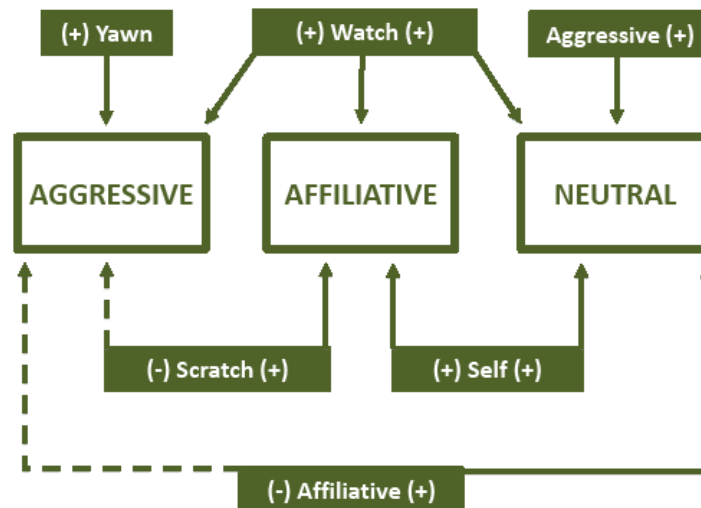
6.4.6 SUMMARY OF RESULTS

Five analyses within this chapter addressed behavioural predictors of chimpanzee introduction outcomes. When examining the visual access period, the majority of the time the chimpanzees avoided the introduction area, followed by exhibiting neutral and aggressive behaviours, with affiliative behaviours being the least frequently observed. None of the social behaviours during the visual access period (i.e. aggressive, affiliative, and neutral) were able to significantly predict introduction outcomes. Personality profiles varied across all chimpanzees and had the most predictive power regarding introduction outcomes. Twelve significant models revealed that aggressive behaviours were predicted by Dominance (positive correlation), Agreeableness (negative correlation), and Extraversion (negative); affiliative behaviours were predicted by Conscientiousness (negative) and Neuroticism (negative); and neutral behaviours were predicted by Conscientiousness (positive), Extraversion (negative), Agreeableness (negative), and Neuroticism (negative) personality factors (see Figure 6.5). When watching the video introductions, the chimpanzees watched an average of 12% of the time, accompanied by fairly low rates of SDBs and social behaviours. Within those behaviours, nine significant models revealed that aggressive behaviours were predicted by the percentage of time spent watching (positive) and rates of scratching (negative), yawning (positive) and exhibiting affiliative behaviours

(negative); affiliative behaviours were predicted by the percentage of time spent watching (positive) and rates of scratching (positive) and self grooming (positive); and neutral behaviours were predicted by the percentage of time spent watching (positive) and rates of self grooming (negative) and exhibiting aggressive (positive) and affiliative (positive) behaviours (see Figure 6.5).



(A) Personality factors predicting social behaviours.



(B) Video introduction behaviours predicting social behaviours.

Figure 6.5. Flow chart summarizing the (A) personality factors and (B) video introduction behaviours that predict social behaviours (aggressive, affiliative, and neutral) during chimpanzee introductions; based on the significant models outlined in Section 6.4.5. White boxes indicate behavioural outcomes; solid boxes indicate predictors; solid arrows indicate positive correlations; and dashed lines indicate negative correlations.

6.5 DISCUSSION

When unfamiliar chimpanzees meet, it is natural for excitement and aggressive behaviours to be exhibited. The battle within the dominance hierarchy had been volatile in the Edinburgh group prior to the arrival of the Beekse Bergen group, but the frequency of wounded chimpanzees increased once the two groups were fully integrated (see Figure 2.3). During managed chimpanzee introductions within this study, after any initial aggression subsides, the keepers looked to other behaviours to signify compatibility and interest from all individuals involved. When chimpanzees move on from aggressive to affiliative or neutral behaviours, this indicates to the keepers that the introduction has progressed in a positive manner and that moving to the next stage would likely be a success (as described in Section 6.3.4.1; Budongo Trail daily records, 2010). In using an individualised management approach (Seres et al., 2001), the keepers rely on their knowledge base of each chimpanzee including details about their personalities and social tendencies when interacting with others. Their expertise is limited to their resident group, so given the findings of this study, additional measures, like formalised personality profiles for incoming individuals, would be beneficial.

6.5.1 VISUAL ACCESS

With gradual introductions that occur in steps (Fritz & Fritz, 1979; Noon, 1991; McDonald, 1994; Alford et al., 1995; Brent et al., 1997; Seres et al., 2001; Fritz & Howell, 2001), the way in which each chimpanzee behaves during the first stages of the introduction process will inevitably play a role in the keepers' overall perceptions of each individual. But without any significant models predicting future introduction outcomes, should the behaviours exhibited during the visual access period be considered in keepers' decisions? Perhaps more importantly, why was there no predictive power?

The differences between the behaviour during visual access and the physical introductions might help to explain why there was no predictive power. Compared to the physical introductions, visual access had 152% more aggressive behaviours, 65% fewer affiliative behaviours, and 42% less neutral behaviours. The higher percentage of aggression is likely related to the nature of the visual access period where the closest access the groups had to each other was through two layers of steel mesh that were two metres apart. Within the protected environment, the chimpanzees had room to show their strength without

having to prove it in a physical fight. This concept of “false bravado” was also evident during some of the dyad and small group introductions when individuals transitioned from protected contact to full contact. For example, Liberius, an 11 year old male from the Edinburgh group was difficult to integrate into the “super group”, likely due to his age and inexperience. During the two aborted attempts to introduce him to out-group females, he was paired first with his mother and then with another familiar female. Both times he exhibited aggression towards the out-group individuals while in protected contact; however, once they had full access to each other, he redirected his aggression to his in-group partner.

Behaviours seen during the visual access period should still be considered in keepers’ decisions because how the chimpanzees behave contribute to their behavioural repertoires in terms of this unique situation. They might also have the potential to shed light on other behaviour patterns not examined in this study (e.g. showing weakness or stability of coalitions within the original groups), however, knowing that there is no predictive power in relation to outcomes, these data indicate that these measures should not be the primary evaluation tool during introductions, or play a large role in management decisions. Further study is required to examine the informative nature of behaviours exhibited during this period. Despite this finding and evidence that familiarity and gradual introductions are not necessarily needed for integration success (Brent et al., 1997), decreased aggression reported over time, as also reported by Bloomsmith et al. (1998), suggest that the early protected contact periods might aid as an outlet from some of the initial aggression.

6.5.2 PERSONALITY PROFILES

Personality studies can be circular in nature, where personality ratings reflect behaviours seen and vice versa (Murray, 2011). This study differs from others by using personality ratings based on the previous behaviour of the groups to predict a new event, the chimpanzee introductions. The 12 significant models within the personality profile category with the highest variance explained by the models (compared to the video introduction models) make this category the most powerful when it comes to predicting introduction outcomes.

6.5.2.1 AGGRESSIVE BEHAVIOURS

Aggression was the behaviour of highest concern as wounding is likely to be more frequent during highly stressful situations, as it was during the introductions in this study (see Figure 2.3). General models, applicable to the behaviour of all individuals, were able to predict behaviour towards males and out-group members, while a more detailed model was able to predict elevated aggression by low-ranked individuals towards in-group individuals.

Individuals who score more highly on Dominance are more likely to be aggressive towards males, but it is not simply about rank. Even though introductions involving males might be similar to those involving high-ranking individuals because of their generally high levels of aggression, this model did not apply to high-ranking individuals meeting males or to anyone meeting high-ranked individuals. It seems reactions were determined predominantly by sex rather than rank. This might imply that when chimpanzees cannot easily identify high-ranking individuals, aggression is avoided.

Meeting out-group individuals is the essence of the introduction process, so naturally aggression is expected in these circumstances. However, once again Dominance did not play a role in the model. Not surprisingly, individuals scoring low on Agreeableness were more likely to be aggressive to out-group individuals than those with higher levels of Agreeableness. Defined by traits like conventional and sympathetic, it makes sense that those who score low on those traits would react negatively to meeting new individuals. If they do not stay within the social rules of the group or act considerate and kind towards others, when challenged with meeting a group of unfamiliar chimpanzees, this may lead to increased aggression during uncertain social contexts (de Waal, 1982).

When separating introductions by sex and rank, lower-ranked individuals with low Extraversion scores, were more aggressive towards familiar individuals (i.e. their in-group). Tensions run high during introductions so individuals who infrequently seek the company of other chimpanzees are not likely to excel in the introduction environment. While they will experience similar emotions as the other chimpanzees, not being comfortable interacting with others means it is more likely that they will displace their frustrations and redirect aggression towards familiar, in-group individuals.

6.5.2.2 AFFILIATIVE BEHAVIOURS

Affiliation, a desirable behaviour to see during introductions, is difficult to predict based on personality profiles. Models examining all individuals predicted that those with low scores of Conscientiousness would be affiliative towards females and low-ranking individuals. When meeting females, individuals with low scores on Conscientiousness were more affiliative and when meeting low ranks, individuals who also scored low on Neuroticism in addition to low Conscientiousness, were more affiliative. Overall having traits like low Conscientiousness (reckless and distractible) and low Neuroticism (unemotional and cool) might lead individuals to be more affiliative to females and low ranks because they are not as much of a perceived threat to social dominance as other individuals.

6.5.2.3 NEUTRAL BEHAVIOURS

Neutral behaviours, another desirable behaviour constellation, were frequently predicted by Conscientiousness; the more conscientious an individual's personality, the more likely they were to be neutral in an introduction. General models were able to predict behaviour towards females, males, low ranks, in-and out-groups while more detailed models were able to predict the neutral behaviours of females to low ranks and of males to females.

While personality scores high in Conscientiousness played a role in all but one model predicting neutral behaviours, Extraversion, Agreeableness, and Neuroticism were included as secondary predictors, all of which included low scores. Individuals who score high on Conscientiousness are likely to be more neutral towards males and in-group members suggesting that being perceptive, dependable, and careful (among other traits) allows you to respond appropriately to situations that have the potential for aggression (i.e. males), as opposed to those that are not threatening (i.e. in-group). When separating the sexes and the ranks, males with high Conscientiousness scores tended to be more neutral towards females. Building relationships with females to potentially increase mating opportunities is an activity that attentive and patient males would be more likely to exploit.

High Conscientiousness scores combined with low Extraversion scores, indicating a lack of sociability combined with calm evaluation of the situation, can lead to developing neutral relationships with non-threatening individuals (i.e. females and low ranks). When high Conscientiousness is combined with low

Agreeableness, it indicates that those who generally do not try to provide reassurance to others when encountered with the seeming threat of unfamiliar individuals will only feel comfortable behaving neutrally towards certain individuals (i.e. low ranks).

The only model that does not incorporate Conscientiousness revolves around out-group individuals. Those who score low on Neuroticism are more likely to be neutral to out-group individuals. Their personalities indicate that they are cool, stable, and less emotionally reactive; a combination that lends itself to creating a neutral environment.

6.5.3 VIDEO INTRODUCTIONS

The chimpanzees each watched an average of 12% of the video introductions. Even though there were nine significant models within the video introduction category, it is important to note that the behaviours analysed occurred infrequently and were predictive in multiple contexts (i.e. high levels of watching was related to high levels of aggressive, affiliative, and neutral behaviours). Without clear patterns in the variables to predict specific behaviours, it is difficult to generalise these results, therefore each model needs to stand on its own for predicting specific behaviours towards specific groups. Subsequently the value of video introductions as a potential method to help guide physical introductions is not as strong as the personality assessments. There is, however, one model that is worth further discussion.

The behaviours males exhibit while watching video introductions of females is extremely predictive (explaining 76% of the variance) of neutral behaviour towards females during physical introductions. The more males watch and the more aggressive they are, the more neutral they are during the actual physical introductions. This could suggest habituation is occurring; a similar concept to the false bravado of the visual introduction period. A few musings as to the reason for this: Males are possibly over stimulated when watching videos of females and exhibit additional aggression. That, however, would contradict Parr and Hopkins' (2000) research showing chimpanzees behavioural responses were typical of the emotional valence they were viewing. Or perhaps they could be vying for the females' attention as those on video are not attending to the presence of the males.

6.6 SUMMARY AND CONCLUSIONS

To systematically study some of the behavioural measures that keepers rely on to safely manage chimpanzee introductions (i.e. personality and social tendencies when interacting with others) a low-cost, quantifiable measure was developed (video introductions) and tested along with two pre-existing measures: Visual access behaviours and personality profiles. By testing these aspects of the introduction process for their abilities to predict outcomes (i.e. behaviours exhibited towards others during introduction), we were able to verify the use of (a) personality profiles and (b) video introductions as tools that can help guide introductions in a way that might reduce risk. Moreover, these analyses also illustrate that the widely used assessment of individual behaviour when given visual access during introductions is not an effective measure in predicting future introduction behaviours.

Personality profiles had the most predictive power through adjusted R^2 values and number of significant models. The most generalisable personality factor to be aware of when managing introductions with unfamiliar, out-group individuals is Agreeableness; individuals who score low on Agreeableness are likely to be aggressive towards out-group individuals. When considering interactions with in-group individuals, Extraversion scores are particularly helpful as they predict how low-ranked individuals react to members of their own groups. Those with low Extraversion scores are not likely to handle the tension of the introduction environment well and are more likely to become aggressive towards their in-group. We suggest that keepers take extra caution when including individuals who score high on Dominance (males and females) as they are likely to be more aggressive to males (who are more at risk for aggression than high-ranked individuals overall).

Conscientiousness was the most prevalent personality factor in predicting neutral behaviours.

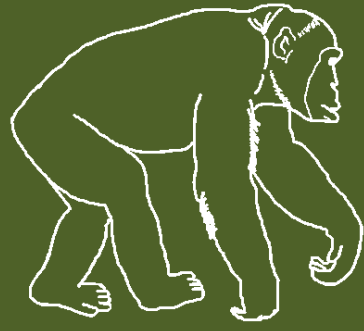
Individuals who score high on Conscientiousness are likely to exhibit neutral behaviours and should be encouraged to be included in as many introduction dyads and small groups as possible to balance out the social dynamics when including more aggressive individuals.

Previous research suggested that the Dominance factor and excitable trait were positively related to agonistic or aggressive behaviour (Pederson et al., 2005; Murray, 1995 as cited in Murray, 2011). While our study supports Pederson's findings, the concept of excitability within the Hominoid Personality

Questionnaire PCA (Weiss et al., 2009) falls under Neuroticism; a factor that does not predict aggression, but does predict neutral behaviour. Additionally, while Extraversion was suggested to be positively linked to affiliative behaviours (Pederson, 2005), this study could only predict aggression and neutral behaviours from low scores of Extraversion. Whether due to situational context differences (e.g. no one has previously studied personality in the context of meeting unfamiliar individuals) or simply statistical analyses (i.e. studies using personality to predict behaviour sometimes rely on correlations: Pederson et al., 2005; Kuhar et al., 2006; Murray, 2011), these findings emphasise the importance of exploring predictability between personality and behaviour in a variety of contexts.

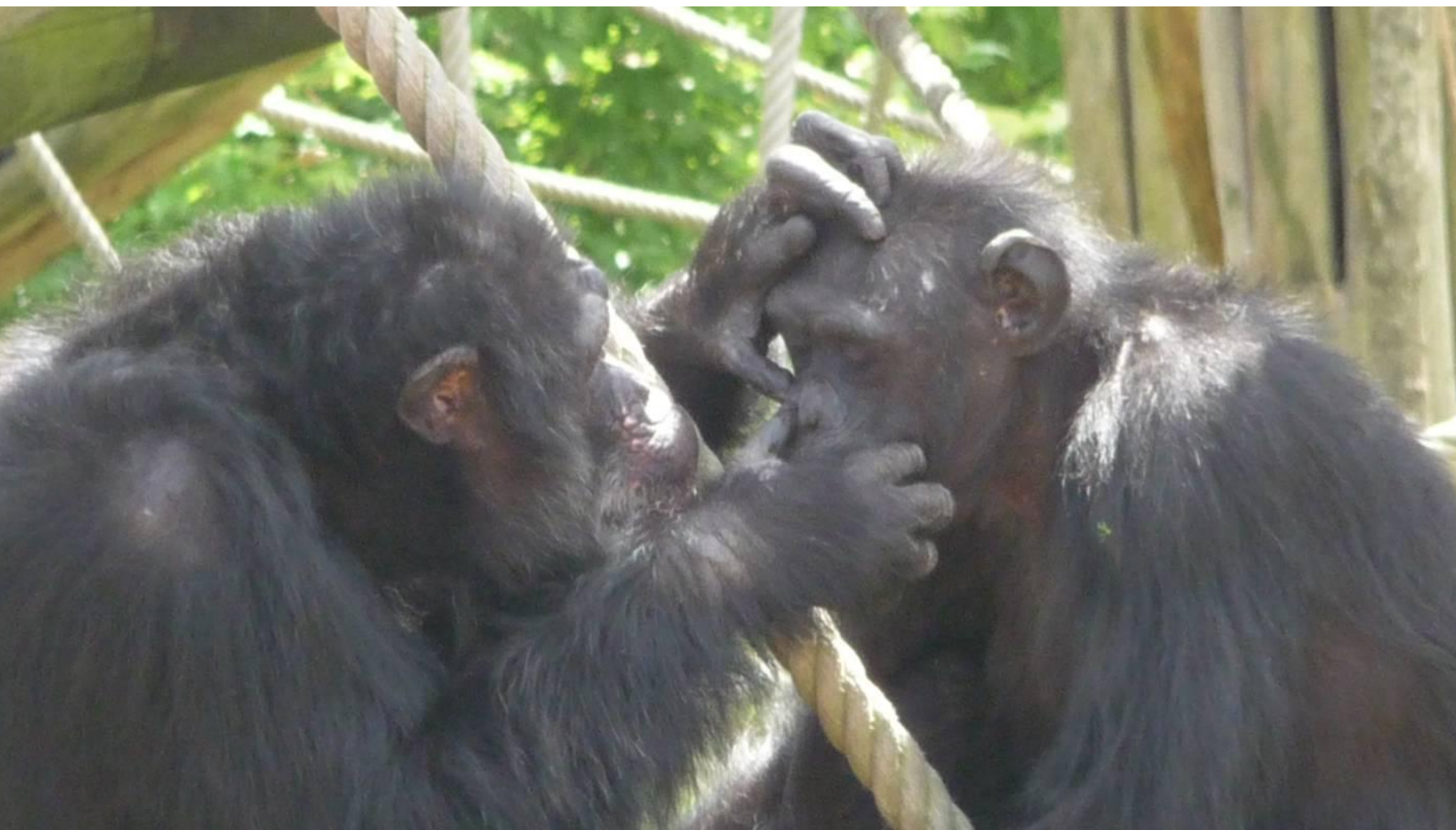
The video introductions included nine significant models predicting introduction outcomes, however, the behaviours analysed occurred infrequently and were predictive in multiple contexts (i.e. high levels of watching was related to high levels of aggressive, affiliative, and neutral behaviours). Generalisation of each variable's meaning was challenging, however one model was particularly interesting. The behaviours males exhibit while watching video introductions of females were predictive (explaining 76% of the variance) of neutral behaviour towards females during physical introductions, possibly adding to the false bravado concept discussed in relation to the visual access period.

While keepers hosting the introductions should be well-versed in all things pertaining to their chimpanzees, if a cross-institutional transfer occurs, bringing in new and unfamiliar chimpanzees, the keepers' knowledge base will be limited. The use of low-cost and relatively brief quantifiable measures of personality assessments, with the potential to develop more simplified versions, to help guide the introduction process is recommended.



CHAPTER 7

WELFARE IMPLICATIONS OF CHIMPANZEE INTRODUCTIONS



WELFARE IMPLICATIONS OF CHIMPANZEE INTRODUCTIONS

7.1 ABSTRACT

Introducing unfamiliar chimpanzees to each other can be a stressful and challenging process. The purpose of this study was to monitor the welfare of the chimpanzees, through self-directed behaviours (SDBs), abnormal behaviour, and social activity, as one group of chimpanzees was introduced to another. SDBs (scratch, rub, and yawn), regurgitation and reingestion (R/R), and allogrooming behaviour of 22 chimpanzees from two separate groups (Edinburgh and Beekse Bergen) were collected over a 7.5 month period. Of specific interest was how SDBs, R/R, and allogrooming changed in response to each phase of the introduction process, including changes in group size, and available space.

Overall there was little impact on welfare, as indicated by our measures. Findings indicate that rates of rubbing decreased from Baseline levels (in their original enclosures) to visual access (immediately before the introduction phase), just before the mixing of the two groups began (Before Mix), then peaked while the groups were merging (Mix) and decreased once all 22 individuals were together (Integration); yawning decreased once the two groups merged (Integration); all other behaviours remained constant.

When examining the impact of having an individual removed from a sub-group compared to a sub-group having a new member (unfamiliar or familiar) introduced, rates of rubbing occurred at higher rates when individuals were removed from a group compared to when they were added, whereas all other behaviours did not change. The results suggest that rubbing may serve as a different function from scratching. Scratching is an indicator of arousal, but may be more associated with contexts in which negative outcomes have previously been experienced, while rubbing may indicate uncertainty that is not negatively valenced. In terms of changes in overall group size, all SDBs increased as individuals were removed from their original subgroup, but remained constant as individuals were added to the new, large group. The number of available rooms was more important than the total amount of available space (m^2) for the frequency of scratching and yawning; which decreased as the number of rooms increased. R/R remained constant throughout, and did not transfer between groups.

We used allogrooming as a measure to examine social cohesion and relationship formation and maintenance. Group density seemed to be more important in determining levels of grooming than the amount of available space (in number of rooms or square metres). Allogrooming increased as group size increased, but remained constant as individuals were removed from subgroups. Allogrooming was also examined in terms of sex, kin, rank, and in-group/out-group differences, but only rank and in-group/out-group status were important factors. While high-ranking individuals groomed others more frequently, recipient rank was not a factor in grooming decisions made by males or females. Individuals preferred to groom in-group over out-group individuals, suggesting grooming was primarily used to maintain existing relationships rather than initiate new ones. The animal management team held welfare as a priority throughout this large-scale chimpanzee introduction and overall, the data suggest that the introduction process did not compromise welfare to a significant degree.

7.2 INTRODUCTION

The welfare implications discussed in this chapter address well-known behavioural indicators of wellbeing (SDBs, R/R, and grooming). Additional information on these introductions, including other behaviours specific to the introductions (e.g. aggressive behaviours) can be found in Chapter 6.

7.2.1 GROUP SIZE

In wild chimpanzees, changes in group size occur because of birth, death (Nishida et al., 2003; Boesch, 1996), or emigration (either permanent or temporary transfer: Nishida, 1979; Pusey, 1979), which normally occurs for females after reaching sexual maturity (age 9.7 to 14, Nishida et al., 2003), but has also been infrequently observed in males (Sugiyama & Koman, 1979). Chimpanzee society has a high fission-fusion dynamic (Kummer, 1971; Aureli et al., 2008) where individuals associate with different individuals in smaller subgroups regularly. In that sense, they are familiar with smaller, regularly changing social units within their group (community), known as parties (Goodall, 1986). Party size frequently changes within a group, with size and duration of associations being dependent upon the activities on offer (Boesch 1996; Newton-Fisher 1999). It is because of the fluid nature of their society that associations and allegiances are so important (de Waal, 1982; Newton-Fisher, 1999). Individuals must attend to their own relationships to gain and maintain status (de Waal, 1982; Dunbar, 1991). The

overall size of a social group determines how complex the social relationships are; individuals must correctly track third party relations and also understand and respond to signals they receive from others in order to maintain their relationships and successfully navigate through their social environment (Dunbar, 1998).

In captivity, a different factor plays a role in group size: animal management. The departure of an individual (even temporarily) can be a stressful event for chimpanzees, particularly when it is unexpected (Anderson, 2011; Gregory, personal communication, 2010) and this is a likely component of chimpanzee introductions. Long gaps may occur between introductions of new individuals to a group, but when a large-scale introduction happens, group size changes are frequent yet unexpected. The groups do not know when each individual may leave and they are not necessarily aware of why the individual(s) are leaving the group at all, leading to considerable uncertainty and upheaval within the group as introductions can be a complex and long process (de Waal, 1982).

7.2.2 AVAILABLE SPACE IN CAPTIVITY

An element in the captive management of animals is safely shifting groups between enclosure areas allowing care staff to provide for the animals (e.g. cleaning, maintenance, feeding, etc.; Hosey et al., 2009). As a result, the space (m²) and number of enclosure areas (separate rooms) available often change. Even without the temporary circumstances of the introduction process, husbandry requirements may limit animals to off-exhibit areas for cleaning or maintenance purposes. Zoos in temperate climates inevitably have to deal with the challenges of temperature fluctuations and inclement weather prompting care staff to occasionally limit animal access to indoor areas (e.g. when moats freeze over, as described by de Waal, 1982). Changes in behaviour as a result of limited enclosure access have been studied in non-primate species, for example, when given a choice of enclosures, giant pandas (*Ailuropoda melanoleuca*) decreased pacing, scratching, and door-directed behaviour, in relation to a no choice condition (Owen et al., 2005).

Crowding and available space is suggested to impact primate relationships where high density situations increase the likelihood of social conflict (Judge, 2000). With most captive ape habitats consisting of two or three separate spaces at most, for example, one outdoor enclosure and one indoor enclosure often

with an indoor, off-exhibit area (e.g. Safaripark Beekse Bergen, Blackpool Zoo, Chester Zoo, Henry Vilas Zoo, Kyoto City Zoo, London Zoo, Paignton Zoo, etc.), when an area needs to be closed off for husbandry purposes, this greatly decreases the choices they have regarding location and interactions. However, as Schapiro (2003) aptly pointed out, if socialisation in the wild only fills 10% of a chimpanzee's day (Pruetz & McGrew, 2002), is it desirable to encourage situations in which interactions are unavoidable? Accordingly, previous research has studied the importance of enclosure size (usage: Traylor-Holzer & Fritz, 1985; differences between facilities: Jensvold et al., 2001; Ross et al., 2009) and group density (Nieuwenhuijsen & de Waal, 1982; Aureli & de Waal, 1997; Videan & Fritz, 2007) on the behaviour of chimpanzees, but space and density are not often considered independently of one another. Different strategies are suggested to explain how they cope with conflict situations (i.e. high density) over different time scales. The conflict-avoidance model occurs when social interactions decrease during short-term conflict management (Judge & de Waal, 1993). The tension-reduction model occurs when affiliative behaviours are increased and aggressive behaviours are decreased during long-term conflict management (de Waal, 1989).

Despite the best efforts of care staff to make life as normal and enriched as possible for those going through the process of being introduced to new individuals, it is undeniable that the animals are experiencing life under different circumstances than usual and may respond differently. This study is the first to examine the impact of changes in available space (m^2) and enclosure areas (separate rooms) for chimpanzees as two groups are merged.

7.2.3 INDICATORS OF WELLBEING: SELF-DIRECTED BEHAVIOURS

Self-directed behaviours (SDBs) are also known as displacement behaviours and are considered to be an unconscious redirection of behaviour, often due to anxiety-inducing situations where the animal is uncertain about how to behave (Maestriperieri et al., 1992). Goodall et al. (1979), for example, stated that when chimpanzees come across unfamiliar individuals, an increase in anxiety levels is indicated by an increase in displacement behaviours. These are behaviours that are within the species-typical repertoire but often occur out of context from their expected function or at higher than usual rates, for example chimpanzee scratching (reviewed by Maestriperieri et al., 1992). Several studies in captivity and in the

wild have used SDBs as behavioural indicators of wellbeing in chimpanzees (captive studies: Aureli & de Waal, 1997; Baker & Aureli, 1997; Leavens et al., 2001; Troisi, 2002; field studies: Itakura, 1993; Castles et al., 1999; Kutsukake, 2003a; Hockings, 2007).

The most commonly reported forms of SDBs in chimpanzees are scratch, rub, self groom, and yawn (see Chapter 3, section 3.2.3 for additional details). Leavens et al. (2001) proposed that self-directed touches to the face (i.e. rub), have a different motivational drive than other SDBs, though not many studies have highlighted this behaviour in their analyses, so the motivation behind the behaviour remains unclear.

Scratch, for example, has been well studied and increases are linked to social changes (e.g. group density and neighbour vocalisations) that have the potential to produce negative outcomes (Aureli & de Waal, 1997; Baker & Aureli, 1997). However, to date, SDBs have not been used to examine uncertainty in relation to the introduction process.

7.2.4 REGURGITATION AND REINGESTION

Regurgitation and reingestion (R/R) is defined as the “voluntary retrograde movement of food and/or fluid from the esophagus or stomach into the mouth, the hands, or a substrate, followed by subsequent consumption of the regurgitant” (Lukas, 1999, pp 238-298). It is exhibited by several non-human primates, most notably chimpanzees and gorillas (Struck et al., 2007). Although the behaviour has not been reported in the wild (Baker & Easley, 1996), Zeller (1991) found that out of four professions that work with exotic animals (i.e. zoo keepers, veterinarians, field researchers, and laboratory workers), only laboratory workers categorised R/R as an ‘abnormal’ behaviour in captive chimpanzees.

Not only does the behaviour have the potential to negatively impact the time budget of animals and their psychological health, but may also negatively impact physical health, for example, out of the 13 chimpanzees observed by Baker & Easley (1996), two never performed R/R, nine performed R/R between 0.3% and 7.9% of the time, and one was observed performing R/R 31% of the time. Even though it is not yet known if R/R affects the health of captive gorillas (Lukas, 1999), it was recently reported that stomach acid is regurgitated (Hill, 2007). This suggests that if high acidity levels in the esophagus have the same detrimental effect in gorillas as it does in humans, chronic repetition of this behaviour could produce health problems.

While no study has found a single factor underlying the behaviour, R/R is suggested to serve as an adaptive response to the stressors of captivity (e.g. space restrictions, diet, boredom, lack of choice and control, stress, etc.), as enjoyment (e.g. re-eating enjoyable foods), or as necessity (e.g. after R/R the nutritional content might have changed or to prolong the feeling of being full) (as reviewed by Lukas, 1999). Significant variation of R/R across eight groups of chimpanzees and 21 groups of rhesus macaques (*Macaca mulatta*) also suggested that the behaviour might be transferable across individuals through social learning (Hook et al., 2002). Human interaction (Baker, 2004) and dietary changes (as reviewed by Lukas, 1999; Struck et al., 2007) have been shown to decrease rates of R/R and anecdotal evidence suggested that these may eliminate the behaviour all together (as reviewed by Lukas, 1999; Catlow, personal communication, 2010), but no systematic approach to the elimination of the behaviour has been reported. We include R/R in this study as it was present in the incoming group (BB) and we were keen to monitor any changes in the frequency or spread of the behavior during the introduction process.

7.2.5 ALLOGROOMING

7.2.5.1 DEFINITION AND PURPOSE

Allogrooming is defined as “picking through hair or at skin of another individual and removing debris with hands and/or mouth and does not include pulling hair” (Ross & Lukas, 2001) and is an important part of daily activities for chimpanzees, representing about 6.2% of their day (Goodall, 1965; Wrangham, 1977, as cited in Dunbar, 1991). The behaviour is suggested to serve as two co-occurring functions: (1) to enhance hygiene through maintenance of the body surface (e.g. removal of parasites), and (2) to enhance relationships and form alliances where grooming can serve as social currency (Dunbar, 1991; McGrew, 2004). Baker and Aureli (2000), on the other hand, suggested that allogrooming served as a way to alter relationships rather than being able to enhance them, noting that the first instance between unfamiliar individuals could mediate a difficult situation; while aggression was hindered, no relationship was present with affiliation (Baker, 1992 as cited in Baker & Aureli, 2000).

7.2.5.2 GROUP SIZE

It is well known that allogrooming is correlated with group size; as species-typical group size increases, so does the amount of allogrooming (Dunbar, 1991). It is important to note that increased time spent grooming does not necessarily relate to a need to groom more individuals, but to potentially intensify existing bonds, making relationships more valuable within larger groups. The relationship between group size and grooming has been explored for differences between rather than within species, prompting the need for additional research on within species variations. While researchers have performed detailed examinations of allogrooming in relation to primate grooming cliques and clusters, previous work has not included details of the relationship between allogrooming and group size within a newly forming group. For example, male chimpanzees groom longer in smaller clusters and females groom longer in larger clusters (Nakamura, 2003) and grooming equity in relation to group size, where equity occurred in all combinations except for male-female dyads (Arnold & Whiten, 2003).

7.2.5.3 IN-GROUP VERSUS OUT-GROUP ASSOCIATIONS

In inter-group encounters, residents of a variety of species typically have the upper hand when it comes to winning battles on their own territory (e.g. birds: Nero, 1956; Krebs, 1982; reptiles: McMann, 2000; invertebrates: Davies, 1978; primates: Cheney, 1981) with potential losses being higher for residents. However, a mathematical model suggests that in contests between multiple chimpanzees, individuals should only compete if their allies outnumber the opposing side by a factor of 1.5 (Wilson et al., 2002). This supports evidence from the Kanyawara chimpanzee community in Kibale National Park, Uganda, where male chimpanzees were only willing to defend their own territory if their group had a numerical advantage over their competitors (Wilson et al., 2001).

Associations between chimpanzees are political and strategic (de Waal, 1982; Goodall, 1986; Newton-Fisher, 1999) where allogrooming efforts are rewarded with social support from the groomee and vice versa, regardless of kin status (Hemelrijk & Ek, 1991), with rates of grooming being highest for individuals who were familiar to the groomer (i.e. from within the same natal group; Sugiyama, 1988). The kin-selection hypothesis identifies that benefits of cooperation amongst related individuals could provide both parties with direct and indirect fitness gains (Hamilton, 1964). Research has shown that

support is provided for kin more often than non-kin and extends to grooming relationships (de Waal, 1978).

Intergroup differences in perception have been studied in social psychology for decades focusing on many topics such as group competition (Sherif et al., 1961; reviewed by Brewer, 1979), race (Tajfel, 1959 & 1970), and cultural differences (Campbell, 1967). Groups that are formed for short periods of time become faithfully supportive of their own group (the in-group) when faced with outsiders (the out-group) (Sherif et al., 1961). Recently, non-human primates have been found to exhibit in-group and out-group awareness through facial recognition and by associating novel items with out-group members (rhesus macaques: Mahajan et al., 2011). The patterns found in humans and rhesus macaques for in- and out-group differences would be expected to carry over into the political world of chimpanzees, for example, Campbell and de Waal (2011) have found that the phenomenon of contagious yawning was more likely when yawn stimuli were in-group rather than out-group.

7.2.5.4 DOMINANCE RANK

Group size is suggested to be an important factor in the relationship between dominance hierarchy and grooming (Sambrook et al., 1995) where individuals may benefit from grooming those in high ranks to gain their support and potentially avoid their aggression (Silk, 1982). Across groups in both captivity and the wild with relatively small number of males (range: 3 – 10), rank had no bearing on allogrooming distribution amongst males (captive with no clear alpha male: Hemelrijk & Ek, 1991 (Arnhem Zoo, the Netherlands); wild: Watts, 2000 (Mahale group, Mahale Mountains, Tanzania with data from Nishida & Hosaka, 1996); Arnold & Whiten, 2003 (Sonso group, Budongo Forest, Uganda)), but did have a positive effect on the frequency of females grooming males in captivity (Hemelrijk & Ek, 1991). Whereas a group with a much large number of males (range: 22-24; Ngogo group, Kibale National Park, Uganda) found that rank influenced allogrooming where lower ranking individuals groomed higher ranking individuals and higher ranking males had the most grooming partners compared to other males (Watts, 2000).

7.2.6 STUDY AIMS

This study aimed to assess welfare through behavioural indicators of wellbeing during the largest chimpanzee introduction attempted to date. By examining behavioural indicators of uncertainty and

social cohesion throughout the introduction process (including data from before one group of chimpanzees was transported to meet a second group through four months after the groups merged), this study was explored in seven analytical categories in which we identified the following hypotheses:

ANALYSIS 1: PHASES OF THE INTRODUCTION PROCESS

(a) SDBs, (b) R/R, and (c) allogrooming would increase across the phases of the introduction process as the chimpanzees continually encountered constantly changing situations.

(d) SDBs and (e) R/R would return to Baseline levels after integration but (f) allogrooming would remain at higher level due to larger overall social group following introductions.

ANALYSIS 2: CHANGES IN GROUP SIZE

(a) SDBs would increase as group size changed in the social upheaval of chimpanzees being removed from their original groups and added to the “super group” (i.e. rates would increase for the subgroups as individuals are removed to become part of the “super group” and rates would increase for the “super group” as individuals are added, see Table 7.1).

(b) Rates of SDBs would be higher for groups in which individuals were removed compared to subgroups with individuals added, regardless of group size, because being reunited with familiar individuals may counteract the uncertainty of meeting unfamiliar individuals.

(c) R/R would increase as group size changed during the Integration phase. Moreover, R/R would be higher for the BB subgroups when individuals were removed compared to when individuals were added, regardless of group size.

(d) Allogrooming would increase as group size increased and would decrease as group size decreased during the Integration phase. In addition, Allogrooming would be lower when individuals were removed from a subgroup compared to when individuals were added, regardless of group size.

ANALYSIS 3: AVAILABLE SPACE – ACCESSIBLE ROOMS

(a) SDBs, (b) R/R, and (c) allogrooming would decrease as the number of accessible enclosure areas (i.e. separate rooms, excluding the outdoor area) increased.

ANALYSIS 4: AVAILABLE SPACE – GROUP DENSITY

(a) SDBs and (b) R/R, and (c) allogrooming would decrease as available space increased and group density decreased.

ANALYSIS 5: R/R GROUP TRANSFER

(a) The abnormal behaviour of R/R would transfer across groups: from the Beekse Bergen group (known to exhibit the behaviour prior to arrival at Edinburgh Zoo) to the Edinburgh group (not known to exhibit the behaviour).

ANALYSIS 6: ALLOGROOMING – RELATIONSHIPS BETWEEN RANK AND SEX

(a) Rank would impact upon time spent grooming.

(b) Female and male patterns of allogrooming would differ, regardless of in- or out-group status: Females would groom higher ranking individuals more than lower ranking individuals and males would groom other males more than females would groom males.

ANALYSIS 7: ALLOGROOMING: IN-GROUP/OUT-GROUP

(a) Individuals would allogroom in-group (familiar) individuals (belonging to same original group) more than out-group (unfamiliar) individuals. Following integration, as familiarity increased, out group grooming would become more frequent.

(b) Females would groom out-group individuals more than males would groom out-group individuals.

(c) Those with kin in their group would groom more than those without kin and rates of grooming kin would be higher following group merging.

7.3 METHODS

7.3.1 STUDY ANIMALS

The study animals were two groups of 11 chimpanzees (*Pan troglodytes*) each. Both groups (Edinburgh and Beekse Bergen) were of similar size, sex composition, and age ranges with the Edinburgh group including slightly older individuals. At the onset of the study, March 2010, the Edinburgh group included 5 males and 6 females ranging in age from 11 to 49 years old (mean = 27.73, SE mean = 3.76); the Beekse Bergen group included 6 males and 5 females ranging in age from 13 to 41 years old (mean = 21.64, SE mean = 2.48). Additional information on the group, their management, and housing conditions is described in Chapter 2, General Methods.

7.3.2 APPARATUS

Noldus Observer XT 8.0 software and paper checksheets (see Appendix B3), along with a beeper to mark 30 second intervals (Casio, model #19502115 and an add-on iPhone application called Timer) were used to record data.

7.3.3 RESEARCH DESIGN

Observations comprised a total of 1,122 10-minute sessions (187 hours) over the course of 51 days from 14 March – 27 October 2011. Pilot sessions were conducted prior to data collection to ensure inter-observer agreement on identification and recording methods for multiple observers. All observations were collected between 08:00 and 18:00 hours across five phases of the introduction process: (1) Baseline, (2) Pre-Introductions, (3) Before Mix, (4) Mix, and (5) Integration. See Table 7.1 for definitions of the introduction phases and a timeline of the process. See Table 7.2 for a timeline of when each chimpanzee was added to the “super group”. Baseline data for the Edinburgh group were calculated from the data collected in Chapter 4 (from 2008-2009); Baseline data for the Beekse Bergen group were collected shortly prior to their relocation to Edinburgh Zoo (2010), as listed in Table 7.1.

Table 7.1. Definitions of the introduction phases and a timeline of the process.

Phase	Definition	Dates
Baseline	Before transportation of the Beekse Bergen group to Scotland. The Edinburgh group was observed in Scotland and the Beekse Bergen group was observed in the Netherlands.	ED (2008-2009); BB (14-15 Mar 2010)
Pre-Introductions	The groups had auditory and visual access to each other during the first two weeks of arrival through two, 2" mesh walls (steel) that were 2 metres apart.	20 – 30 Mar 2010
Before Mix	In addition to auditory and visual access, select individuals could also interact through a one, 2" mesh wall (steel) or without a barrier (as organised and supervised by keepers), but always returned to original group at night.	31 Mar – 11 May 2010
Mix	Following successful introductions (determined by observations of affiliative or neutral behaviours) in the off-show area, individuals were moved from their original group into the "super group" consisting of chimpanzees from both Edinburgh and Beekse Bergen groups. (If unsuccessful introductions occurred, individuals were returned to their original groups and were later introduced with the same or a different combination of individuals.)	12 May – 7 Jul 2010
-- Mix-- (individuals removed)	Subsection of Mix where individuals were removed from each group to create the "super group".	12 May – 7 Jul 2010
-- Mix-- (individuals added)	Subsection of Mix where individuals from each group were added to the "super group".	12 May – 7 Jul 2010
Integration	Chimpanzees were fully mixed and had access to the entire Budongo Trail enclosure (as permitted by the keepers).	7 Jul – end of study (27 Oct 2010)
--Initial Integration-- (1st 20 days)	Subsection of Integration where data was analysed from the first 20 days of the chimpanzees being fully Integration and the last 20 days of the study (used in analysis 2b).	8 – 27 Jul 2010
--Follow-up Integration-- (3 months into Integration, last 20 days of study)	Subsection of Integration where data was analysed from the last 20 days, six months after the Beekse Bergen chimpanzees arrived in Edinburgh (used in analyses 1d, 1e, and 5).	8 – 27 Oct 2010

Table 7.2. Timeline of when each chimpanzee (including original group, sex, and rank (in brackets), see Table 2.2 and Section 2.4.3.2) was added to the “super group”.

Date	Chimpanzees added to “super group”		Ratio of ED to BB in “super group”
	Edinburgh Group (ED)	Beekse Bergen Group (BB)	
12 May 2010	Louis, male (3)	Pearl, female (4)	1:1
16 May 2010	David, male (2)	Heleen, female (9)	2:2
24 May 2010	Emma, female (4) Cindy, female (11)	Eva, female (3) Lianne, female (11)	4:4
26 May 2010	Ricky, male (10)		5:4
1 Jun 2010		Bram, male (6) Rene, male (5)	5:6
23 Jun 2010	Lucy, female (6) Liberius, male (7)		7:6
29 Jun 2010	Kilimi, female (8) Lyndsey, female (9)	Frek, male (7)	9:7
30 Jun 2010		Edith, female (8) Sophie, female (10)	9:9
5 Jul 2010	Qafzeh, male (1)	Paul, male (2)	10:10
7 Jul 2010	Kindia, male (5)	Claus, male (1)	11:11

Note: The introductions occurred in several steps. Each step varied in duration that was specific to the needs those involved. Progression to each step was based on keeper assessment of likely outcomes of the introduction. (1) Individuals selected for one-to-one (or more if appropriate) introduction from both groups. (2) Chimpanzees interacted through a barrier. (3) Chimpanzees interacted in the same enclosure, without a barrier. (4) The individuals already in the “super group” were introduced to the new pair/group (this occurred in incremental batches when the “super group” size was over 4. (5) All individuals involved moved to the “super group” enclosure.

7.3.4 DATA COLLECTION

Focal subject sampling was used to follow each chimpanzee for 10 minutes on each observation day, with 22 sessions balanced across the course of the day. Within each observation session, all-occurrences recording was used to collect data on self-directed behaviours (SDBs) and regurgitation and reingestion (R/R) while instantaneous time sampling (every 30 seconds) was used to record allogrooming, and the status of mixing between groups (see Table 7.3 for definitions). Note that the SDB of self-groom was not used in any analyses due to a lack of IOR across observers. If a chimpanzee went out of sight, the observer tried to find the chimpanzee, or waited for the chimpanzee to come back into view for up to three minutes, after which time the observer started a new observation with a new focal

animal. If an observation session was cut short due to a chimpanzee going out of sight, the observer aimed to complete the session when the individual reappeared in view and any ongoing focal observation session had been completed.

All data were coded in real time between three observers, the primary researcher (Herrelko) and two research assistants (LM and JG). Data for the Baseline condition were collected by the primary researcher from 2008 – 2009 (see Chapter 4). Only SDBs were recorded during the Baseline and Pre-introduction conditions, therefore allogroom analyses only proceeded for the Before Mix, Mix, and Integration phases. Separate from the real-time data collection, individual chimpanzees were numerically ranked and placed into three categories (high, middle, and low) based on qualitative assessments from the researcher, three keepers from Edinburgh Zoo and two keepers from Safaripark Beekse Bergen who worked with the chimpanzees they ranked for at least six months (see Appendix A) based on observations of each individual's interactions within the group (see Table 2.2 and Section 2.4.3.2).

7.3.5 DATA ANALYSIS

7.3.5.1 EVENT AND STATE BEHAVIOURS

Rates⁶ per minute were calculated by dividing event frequency by the duration of the observation sessions (during which the focal animals were always in view). Estimated percentage of time spent exhibiting a behaviour was calculated by dividing the number of point samples of each behaviour by the total number of sample points (Martin & Bateson, 2007). Rates per minute (for events) and estimated percentages (for states) were used to allow for comparisons across all phases, with each individual contributing one mean rate per phase or condition to avoid pseudo-replication of data (Dawkins, 2007). Subject to availability in visible areas during the introduction process, the number of observations per

⁶ SDB data are reported by individual behaviour instead of one category of SDBs. Chapter 4 includes data on one category of SDBs because the individual behaviours were exhibited in similar patterns (noting the rare occasion they were different), but the behaviours did not follow the same patterns in these analyses.

individual for the analyses ranged from 1 to 42 (mean = 10.21, SE = 0.4) (see Appendix C3 for a listing of all observation totals).

7.3.5.2 ANALYTICAL CATEGORIES

Detailed analyses of the Mix phase compare Individuals Removed versus Individuals Added. These categories occurred simultaneously: individuals were being removed from their original groups to be added to the “super group”. The first 11 chimpanzees in the “super group” were observed as individuals were being added and the last 11 chimpanzees in their original groups were observed as individuals were being removed.

Available space was split into two categories: number of rooms and total size (square metres). As the number of rooms increased, so did the size of the available space. To separate the number of rooms in a space from the size of the space, comparable analyses were performed on enclosure size where a relatively equal number of accessible rooms were represented in each size category (i.e. 1-3 enclosure areas were included in the 21-168 (low) square metre range and 2-3 enclosure areas were included in the 240-360 (high) square metre range; the outdoor area was omitted from both categories). The outdoor area was excluded from analyses to avoid the confounds of the drastically different environment and to allow for comparisons of like-for-like areas.

Allogrooming data were presented in two forms, in terms of overall allogrooming followed by analyses of specific characteristics which are presented (e.g. in-group versus out-group) in terms of percentage of overall allogrooming (i.e. out of 100% of their total time allogrooming). All but one chimpanzee was observed participating in grooming (Cindy). Subsequently the analyses looking at characteristics in terms of overall allogrooming were limited to 21 individuals.

7.3.5.3 INTER-OBSERVER RELIABILITY

Inter-observer reliability was tested between the primary observer and each research assistant on two occasions. The following behaviours reached acceptable levels (i.e. $r > 0.7$ and $n \geq 5$) of reliability (Martin & Bateson, 2007): scratch (LM: $r = 0.83$, $n = 43$; JG: $r = 0.94$, $n = 34$), rub (LM: $r = 0.91$, $n = 37$; JG: $r = 0.86$, $n = 36$), yawn (LM: $r = 0.81$, $n = 14$; JG: $r = 0.82$, $n = 7$), and allogroom (LM: $r = 0.98$, $n = 5$; JG:

$r = 1.0$, $n = 5$). Regurgitation and reingestion occurred infrequently ($n = 2$ for both observer pairs), but was a distinct behaviour that was always recognizable ($r = 1.0$). While typical IOR rules would normally exclude this behaviour from analyses, the presence of the abnormal behaviour (or lack thereof) was deemed too important to exclude. For dominance ranking IOR, see Chapter 2.

7.4 RESULTS

7.4.1 ANALYSIS 1: PHASES OF THE INTRODUCTION PROCESS

7.4.1.1 (A) SDBS THROUGHOUT THE INTRODUCTION PROCESS

A Friedman's ANOVA indicated that scratching rates were low and did not significantly increase across the phases of the introduction process ($\chi^2(4) = 7.89$, $p = 0.096$, $n = 22$, see Figure 7.1): Baseline (median = 0.35), Pre-Introductions (median = 0.30), Before Mix (median = 0.33), Mix (median = 0.44), and Integration (median = 0.37).

Rubbing differed across phases (Friedman's ANOVA, $\chi^2(4) = 19.07$, $p = 0.001$, $n = 22$, see Figure 7.1) Baseline (median = 0.20), Pre-Introduction (median = 0.10), Before Mix (median = 0.15), Mix (median = 0.19), and Integration (median = 0.11). Wilcoxon signed-rank tests, where the alpha criterion was reduced to 0.01 to correct for multiple tests, showed that rubbing was significantly higher during the Baseline phase than during the Before Mix phase ($T = 57$, $r = -0.48$, $p = 0.002$) and the Integration phase ($T = 39$, $r = -0.61$, $p = 0.005$), and rubbing during the Mix phase was significantly higher than the Before Mix phase ($T = 220$, $r = 0.65$, $p = 0.002$) and the Integration phase ($T = 10$, $r = -0.81$, $p < 0.001$). Rubbing, however, did not significantly differ between: the Baseline and the Pre-Introduction phase ($T = 64$, $r = -0.33$, $p = 0.13$); the Baseline and the Before Mix phase ($T = 112$, $r = -0.10$, $p = 0.64$); the Pre-Introduction and the Before Mix phase ($T = 106$, $r = -0.14$, $p = 0.51$); the Pre-Introduction and the Mix phase ($T = 180$, $r = 0.37$, $p = 0.08$); the Pre-Introduction and the Integration phase ($T = 96$, $r = -0.21$, $p = 0.32$); the Before Mix and the Integration phase ($T = 103$, $r = -0.16$, $p = 0.45$).

Yawning was infrequent, but significantly differed across the phases (Friedman's two-way ANOVA, $\chi^2(4) = 18.46$, $p = 0.001$, $n = 22$, see Figure 7.1), Baseline (median = 0.00, mean = 0.06, SE = 0.03), Pre-Introduction (median = 0.00, mean = 0.04, SE mean = 0.01), Before Mix (median = 0.02), Mix (median =

0.04), and Integration (median = 0.03). Wilcoxon signed-rank tests with a Bonferroni correction showed that yawning occurred significantly more during the Mix phase compared to the Integration phase ($T = 34, r = -0.64, p = 0.003$). All other comparisons were not significant: Baseline versus Pre-Introductions ($T = 23, r = -0.10, p = 0.65$), Before Mix ($T = 103, r = 0.16, p = 0.45$), Mix ($T = 176, r = 0.34, p = 0.11$), and Integration ($T = 159, r = 0.22, p = 0.29$); Pre-Introductions versus Before Mix ($T = 115, r = 0.27, p = 0.20$), Mix ($T = 169, r = 0.29, p = 0.17$), and Integration ($T = 87, r = -0.21, p = 0.32$); Before Mix versus Mix ($T = 162.5, r = 0.25, p = 0.242$) and Integration ($T = 87, r = -0.21, p = 0.32$). The pattern of yawning does not clearly reflect the differing phases of introduction as only one comparison reached significance; the Mix phase had more yawning than the Integration phase.

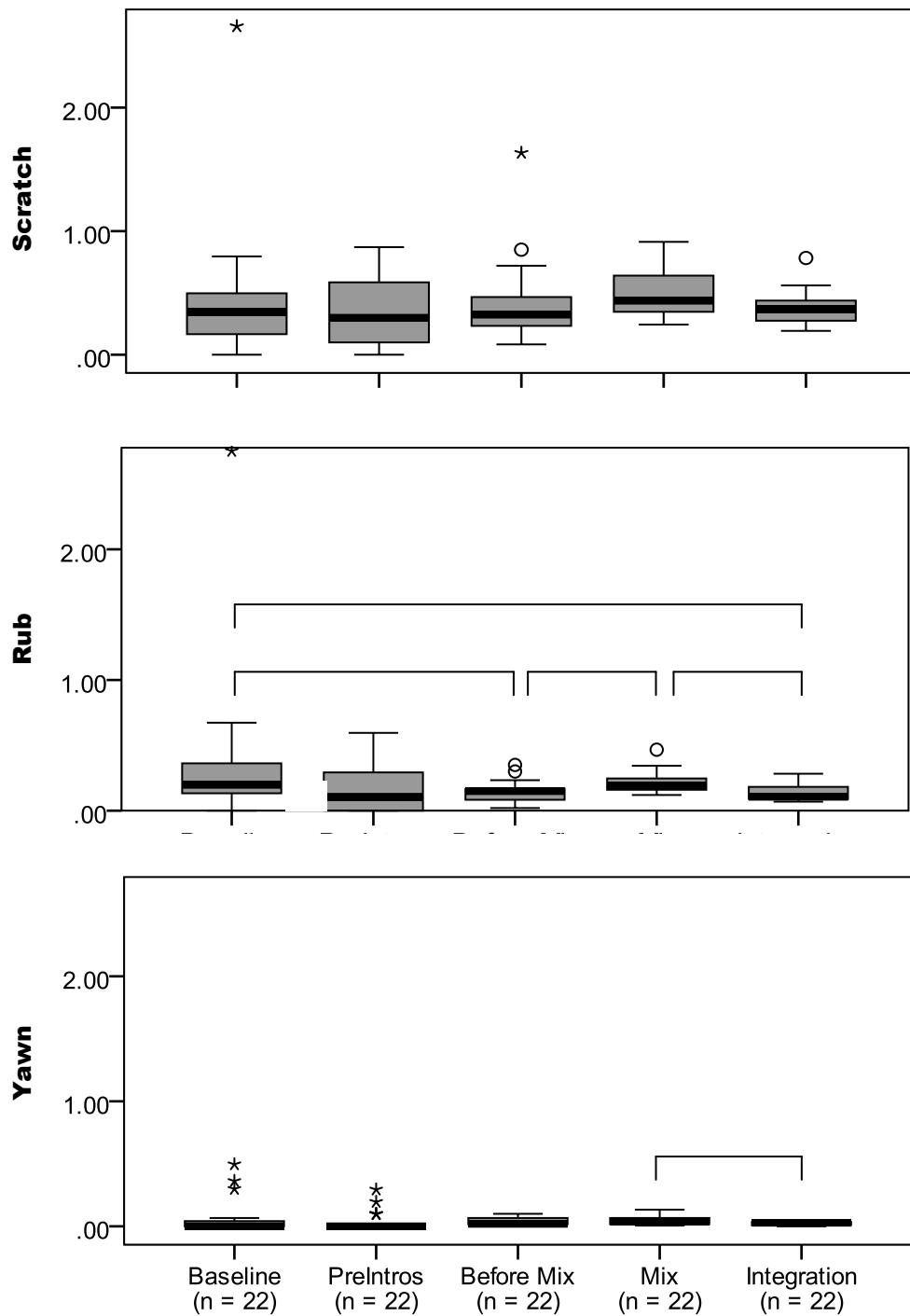


Figure 7.1. A comparison of the median and interquartile range (IQR) of scratch (top), rub (middle), and yawn (bottom) rates per minute across the five introduction phases: Baseline, Pre-Introductions, Before Mix, Mix, and Integration. Whiskers represent 5th and 95th percentiles; adjoining brackets highlight significant differences; circles and asterisk show outliers. The outliers represent: Scratch – Baseline: Frek (2.66); Before Mix: Sophie (0.85) and Cindy (1.63); and Integration: Cindy (0.78). Rub – Baseline: Frek (2.75); Before Mix: Cindy (0.30) and Emma (0.35); and Mix: Liberius (0.47). Yawn – Baseline: Emma (0.10), Kindia (0.30), Eva (0.36), Bram (0.50); Pre-Introductions: Edith (0.10), Lucy (0.10), Liberius (0.20), and Paul (0.29).

7.4.1.2 (B) R/R THROUGHOUT THE INTRODUCTION PROCESS

R/R did not increase across phases (Friedman's two-way ANOVA, $\chi^2(4) = 4.11$, $p = 0.39$, $n = 11$, see Figure 7.2): Baseline (median = 0.1, mean = 0.14, SE mean = 0.05), Pre-Introduction (median = 0.00, mean = 0.11, SE mean = 0.09), Before Mix (median = 0.00, mean = 0.06, SE mean = 0.03), Mix (median = 0.01, mean = 0.02, SE mean = 0.01), and Integration (median = 0.01, mean = 0.03, SE mean = 0.01) phases. .

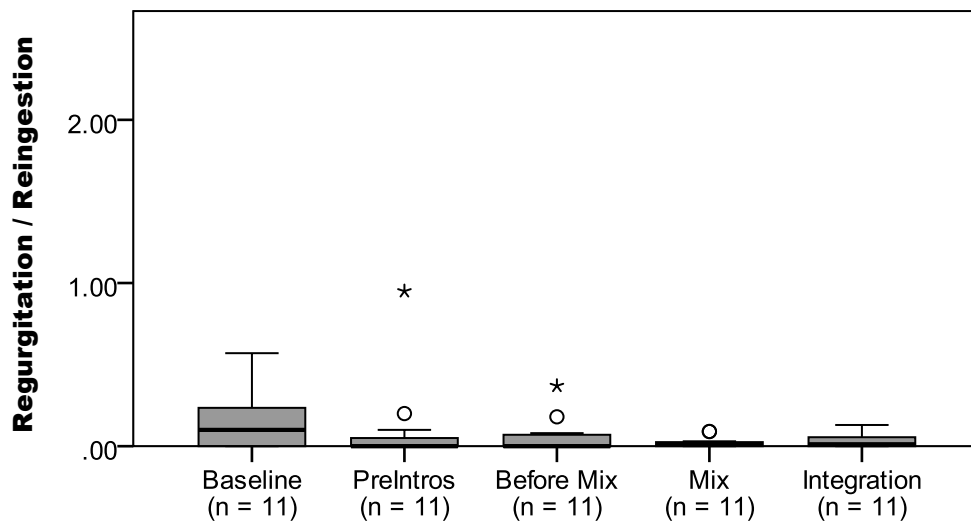


Figure 7.2. A comparison of the median and interquartile range (IQR) of the regurgitation and reingestion rate per minute across the five introduction phases: Baseline, Pre-Introductions, Before Mix, Mix, and Integration. Whiskers represent 5th and 95th percentiles; circle and asterisk show outliers with numbers to represent outlier data points. The outlier(s) in the Pre-Introduction phase represents Frek (0.2) and Sophie (0.95), in the Before Mix phase represents Sophie (0.18) and Lianne (0.37), and in the Mix phase represents Paul (0.09) and Frek (0.09).

7.4.1.3 (C) ALLOGROOMING THROUGHOUT THE INTRODUCTION PROCESS

Estimated percentage of time spent allogrooming (both allogrooming others and being groomed) was significantly different across phases (Friedman's two-way ANOVA, $\chi^2(2) = 12.217$, $p = 0.002$, $n = 21$, see Figure 7.3): Before Mix (median = 1.67), Mix (median = 7.03), and Integration (median = 8.59). Wilcoxon signed-rank tests with a Bonferroni correction showed no differences; Before Mix was not statistically different from Mix ($T = 136$, $r = 0.25$, $p = 0.247$), Mix was not statistically different from Integration ($T = 164.5$, $r = 0.36$, $p = 0.089$) and Before Mix was not statistically different from Integration ($T = 182$, $r = 0.49$, $p = 0.021$).

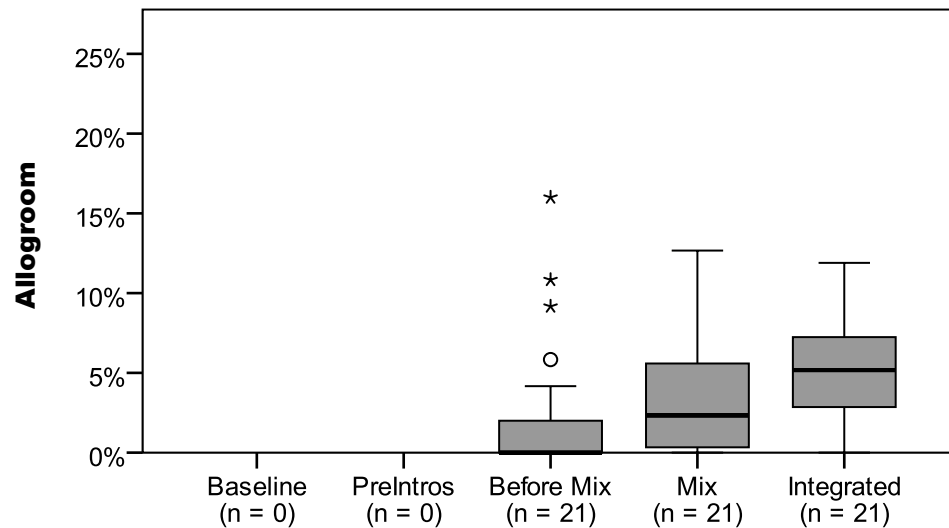


Figure 7.3. A comparison of the median and interquartile range (IQR) of the estimated percentage of time spent allogrooming across three introduction phases: Before Mix, Mix, and Integration. Data for Baseline and Pre-Introduction phases were not collected prior to the arrival of the new group. Whiskers represent 5th and 95th percentiles; circles and asterisk show outliers. The outliers in the Before Mix phase represent Claus (5.83%), Heleen (9.17%), Liberius (10.83%), and Eva (16%).

7.4.1.4 (D) SDBS AFTER INTEGRATION

Scratching remained at baseline levels and did not significantly differ over time as the chimpanzees had time to settle into the new “super group” situation three months after the original groups merged (Friedman’s two-way ANOVA, $\chi^2(2) = 0.82$, $p = 0.66$, $n = 22$, see Figure 7.4): Baseline (median = 0.35, mean = 0.43, SE mean = 0.12), Initial Integration (median = 0.32, mean = 0.37, SE mean = 0.05), Follow-up Integration (median = 0.32, mean = 0.37, SE mean = 0.05).

Rubbing was significantly different across phases (Friedman’s two-way ANOVA, $\chi^2(2) = 10.78$, $p = 0.005$, $n = 22$, see Figure 7.4): Baseline (median = 0.2), Initial Integration (median = 0.12), and Follow-up Integration (median = 0.07). Wilcoxon signed-rank tests with a Bonferroni correction showed that Baseline was significantly higher than Initial Integration, ($T = 40$, $r = -0.34$, $p = 0.005$); Baseline was significantly higher than Follow-up Integration ($T = 29$, $r = -0.39$, $p = 0.002$); Initial Integration was significantly higher than Follow-up Integration ($T = 38.5$, $r = -0.33$, $p = 0.007$).

Yawning remained at baseline levels and did not significantly differ over time (Friedman’s two-way ANOVA, $\chi^2(2) = 2.41$, $p = 0.3$, $n = 22$, see Figure 7.4): Baseline (median = 0.00, mean = 0.06, SE mean = 0.03), Initial Integration (median = 0.02, mean = 0.03, SE mean = 0.01), Follow-up Integration (median = 0.01, mean = 0.02, SE mean = 0.01).

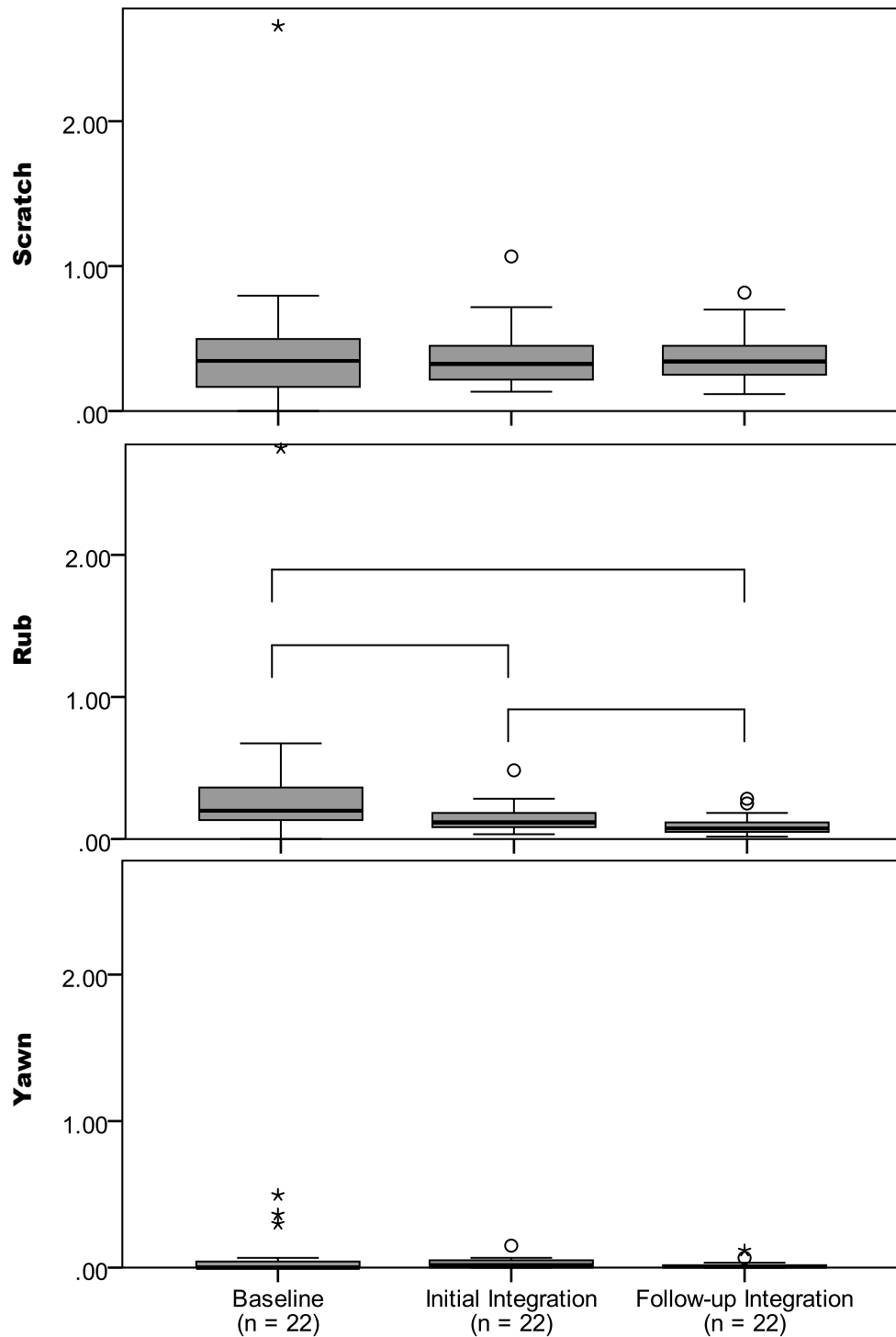


Figure 7.4. A comparison of the median and interquartile range (IQR) of scratch (top), rub (middle), and yawn (bottom) rates per minute comparing Baseline, Initial Integration, and Follow-up Integration (see Table 7.1). Whiskers represent 5th and 95th percentiles; adjoining brackets highlight significant differences; circles and asterisk show outliers. The outliers represent: Scratch – Baseline: Frek (2.66), Initial Integration: Cindy (1.07), Follow-up Integration: Cindy (0.82). Rub – Baseline: Frek (2.75), Initial Integration: Frek (0.48); Follow-up Integration: Emma (0.25) and Liberius (0.28). Yawn – Baseline: Kindia (0.3), Eva (0.36), and Bram (0.50); Initial Integration: Frek (0.15); Follow-up Integration: Paul (0.07) and Lianne (0.12).

7.4.1.5 (E) R/R AFTER INTEGRATION

Since the scores for the Initial Integration and Follow-up Integration phases were both zero, a single comparison of the Baseline (median = 0.10, $n = 11$) and Integration phases (median = 0, $n = 11$) was performed. R/R occurred significantly higher during the Baseline phase (Wilcoxon signed-rank test, $T = 0$, $r = -0.47$, $p = 0.03$, see Figure 7.5).

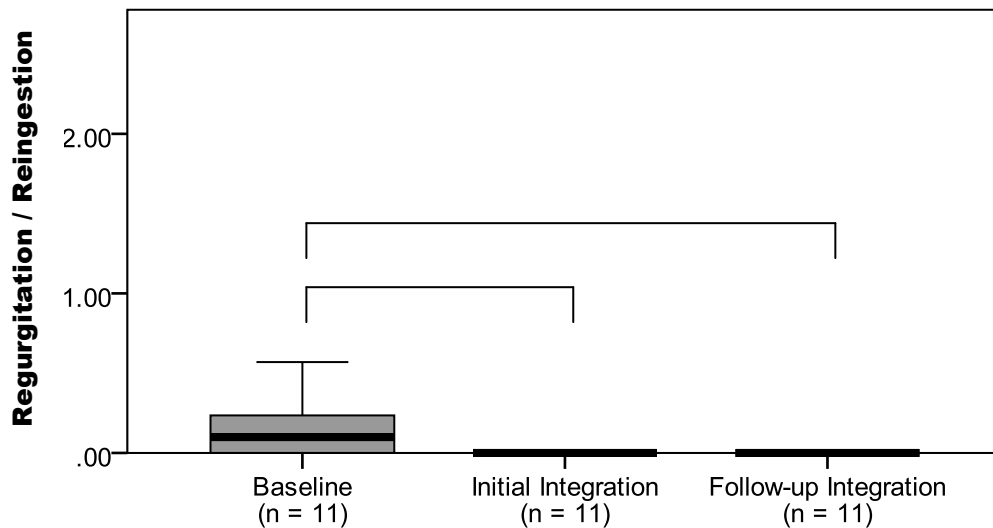


Figure 7.5. A comparison of the median and interquartile range (IQR) of the regurgitation and reingestion rates per minute comparing Baseline, Initial Integration, and Follow-up Integration (see Table 7.1). Whiskers represent 5th and 95th percentiles; adjoining brackets highlight significance.

7.4.1.6 (F) ALLOGROOMING AFTER INTEGRATION

Allogrooming did not significantly differ over time (Wilcoxon signed ranks test, $T = 69$, $r = -0.20$, $p = 0.18$, see Figure 7.6): Initial Integration (median = 4.17, mean = 6.63, SE mean = 1.78, $n = 21$) and Follow-up Integration (median = 0.83, mean = 3.67, SE mean = 1.03, $n = 21$).

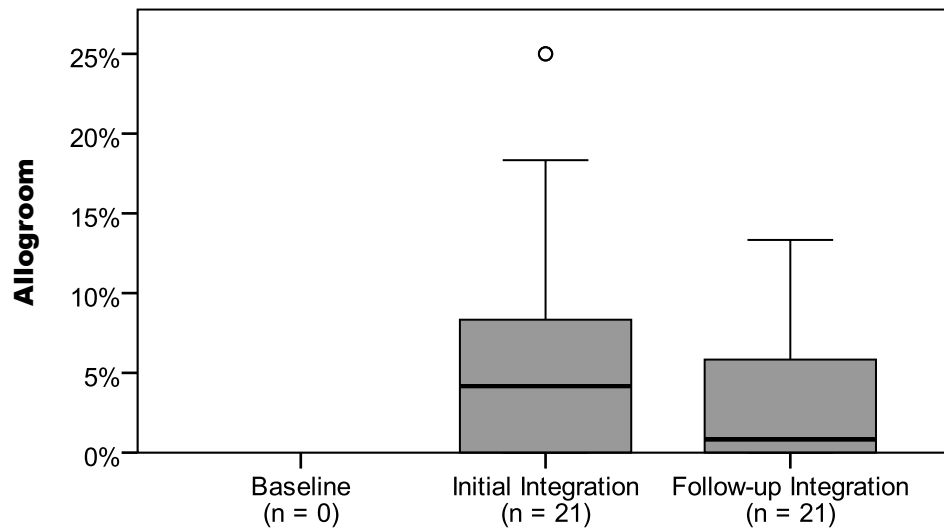


Figure 7.6. A comparison of the median and interquartile range (IQR) of the percentage of time spent allogrooming comparing Initial Integration and Follow-up Integration (see Table 7.1). Baseline rates were not collected (see Section 7.3.5). Whiskers represent 5th and 95th percentiles; circles represent outliers. The outliers for Initial Integration are David (25%) and Ricky (25%).

7.4.2 ANALYSIS 2: GROUP SIZE

The individuals that were to be introduced to each other before joining the “super group” were decided by the animal management team based on many factors. As a result, individuals were removed from each group at an uneven rate. Therefore, as group size changed, the number of individuals in a group was equal to the number of sample points for each group size (see Appendix C3). Two exceptions to this rule exist for the current set of analyses: (1) A total of eight individuals were included for group size 4 because both groups were observed (on separate days) when their original group consisted of four chimpanzees. (2) Only six individuals were included for group size 10 because four observations were completed prior to the start of that day’s introduction and subsequent removal of an individual.

7.4.2.1 (A) SDBS IN RELATION TO CHANGES IN GROUP SIZE

In accordance with the hypothesis, when individuals were being removed from their group (to join the “super group”), scratch, rub, and yawn rates were negatively correlated with group size, SDB rates increased as individuals were removed (Spearman’s correlation coefficient, scratch: $r = -0.757$, $p < 0.001$; rub: $r = -0.707$, $p < 0.001$; yawn: $r = -0.370$, $p = 0.031$, see Figure 7.7). When individuals were being added to the “super group”, scratch, rub, and yawn rates were not significantly correlated with

group size (Spearman's correlation coefficient, scratch: $r = -0.118$, $p = 0.27$; rub: $r = -0.162$, $p = 0.12$; yawn: $r = -0.074$, $p = 0.48$, see Figure 7.8).

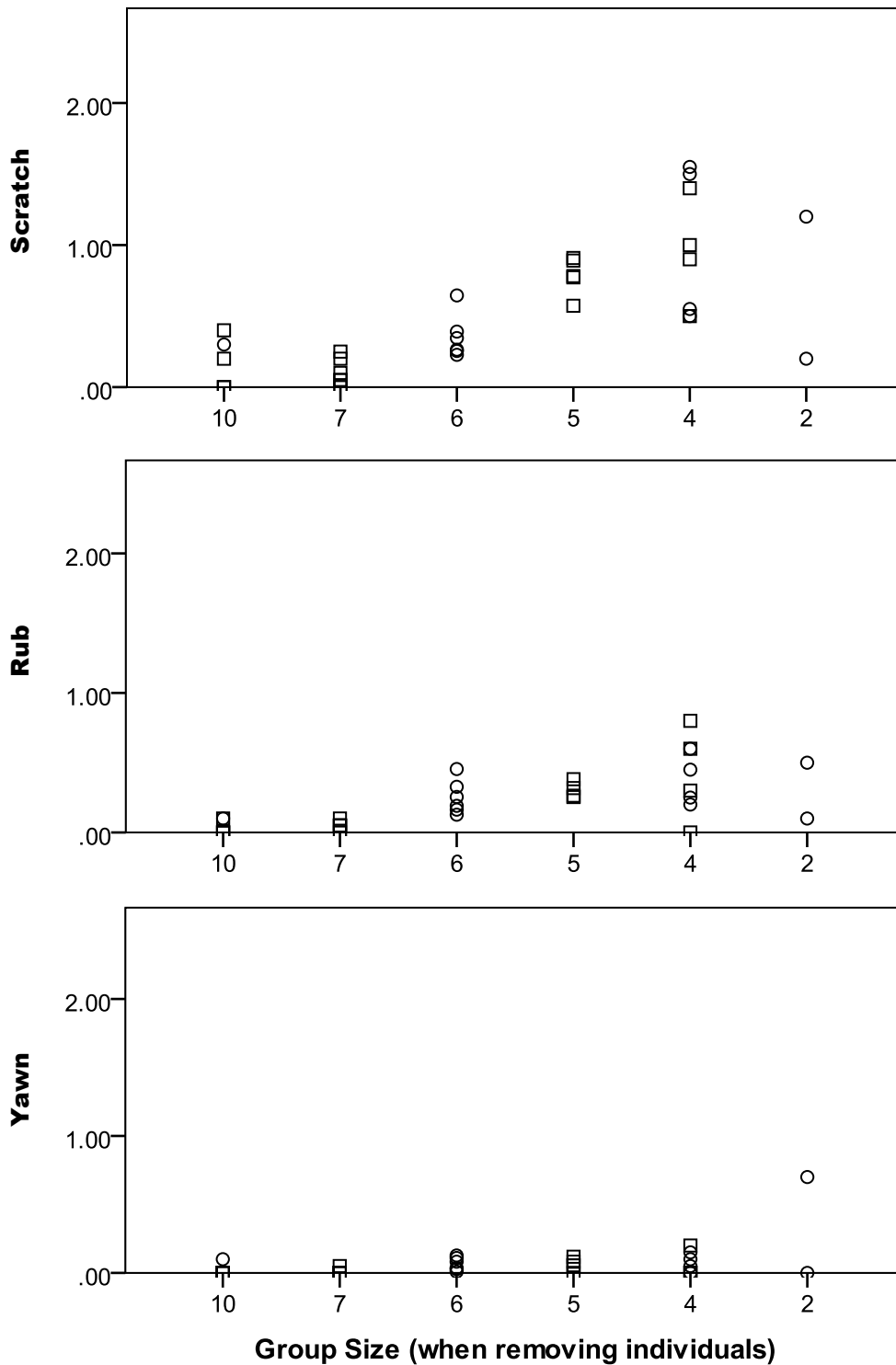


Figure 7.7. Comparisons of group size versus SDB (scratch, rub, and yawn) rates per minute as individuals were removed from their original groups for introduction purposes. Circles represent data points for the Edinburgh group and squares represent values for the Beekse Bergen group. The data include a total of 34 individual averages; see Appendix C3 for sample sizes per group size.

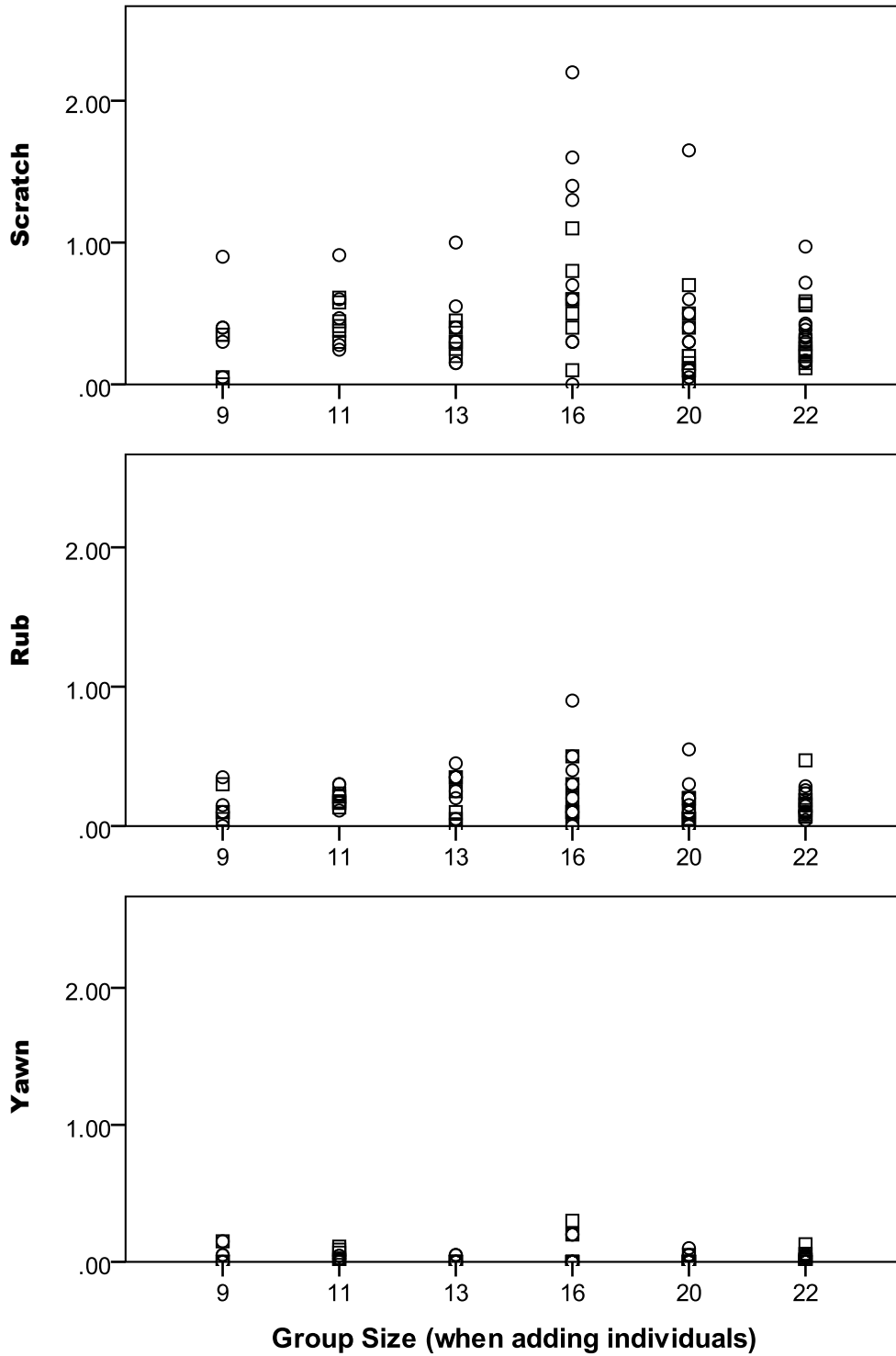


Figure 7.8. Comparisons of group size versus SDB (scratch, rub, and yawn) rates per minute as individuals were added to the “super group” for introduction purposes. Circles represent data points for the Edinburgh group and squares represent values for the Beekse Bergen group. The data include a total of 91 individual averages; see Appendix C3 for sample sizes per group size.

7.4.2.2 (B) SDDBS IN RELATION TO BEING REMOVED OR ADDED TO A GROUP

Rates of scratching did not significantly differ dependent on whether individuals were removed (mean = 0.54, SE mean = 0.06) or added (mean = 0.43, SE mean = 0.05) to a sub group (Independent samples t-test, $t(20) = 1.31$, $p = 0.20$, $N = 11$ see Figure 7.9)

In contrast, rubbing was significantly higher for those left behind when individuals were removed (mean = 0.26, SE mean = 0.03, $n = 11$) compared to individuals who were added to the “super group” (mean = 0.19, SE mean = 0.02, $n = 11$, Independent samples t-test, $t(20) = 2.289$, $p = 0.03$, see Figure 7.9).

Yawning did not significantly differ when individuals were removed (median = 0.07, mean = 0.06, SE mean = 0.01, $n = 11$) from original groups or added to the “super group”, (median = 0.03, mean = 0.36, SE mean = 0.01, $n = 11$, Mann-Whitney U, $U = 33.5$, $z = -1.78$, $p = 0.076$, $r = -0.38$, see Figure 7.9).

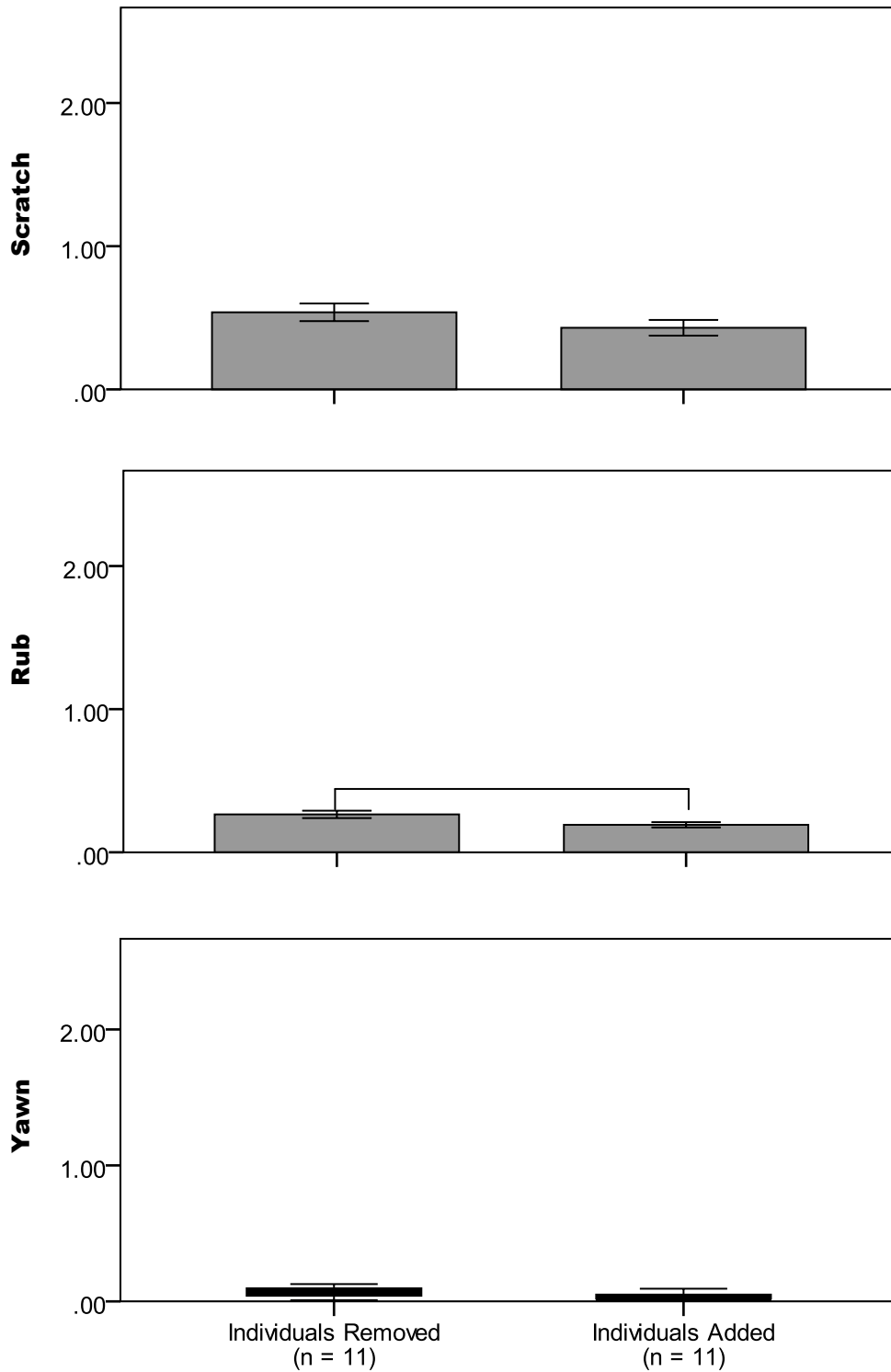


Figure 7.9. A comparison of the mean (+/- 1 SE) scratch and rub rates per minute and median and interquartile range (IQR) of the yawn rate per minute comparing conditions during the introduction process when individuals were removed from their original group to when individuals were added to the “super group”. Whiskers for yawn represent 5th and 95th percentiles; adjoining brackets highlight significant differences.

7.4.2.3 (C) R/R IN RELATION TO CHANGES IN GROUP SIZE

R/R was not significantly correlated with overall group size, regardless of whether individuals were being removed from their original groups or added to the “super group” (Spearman’s correlation coefficient, Individuals Removed: $r = -0.393$, $p = 0.08$ and Individuals Added $r = 0.073$, $p = 0.632$, see Figure 7.10).

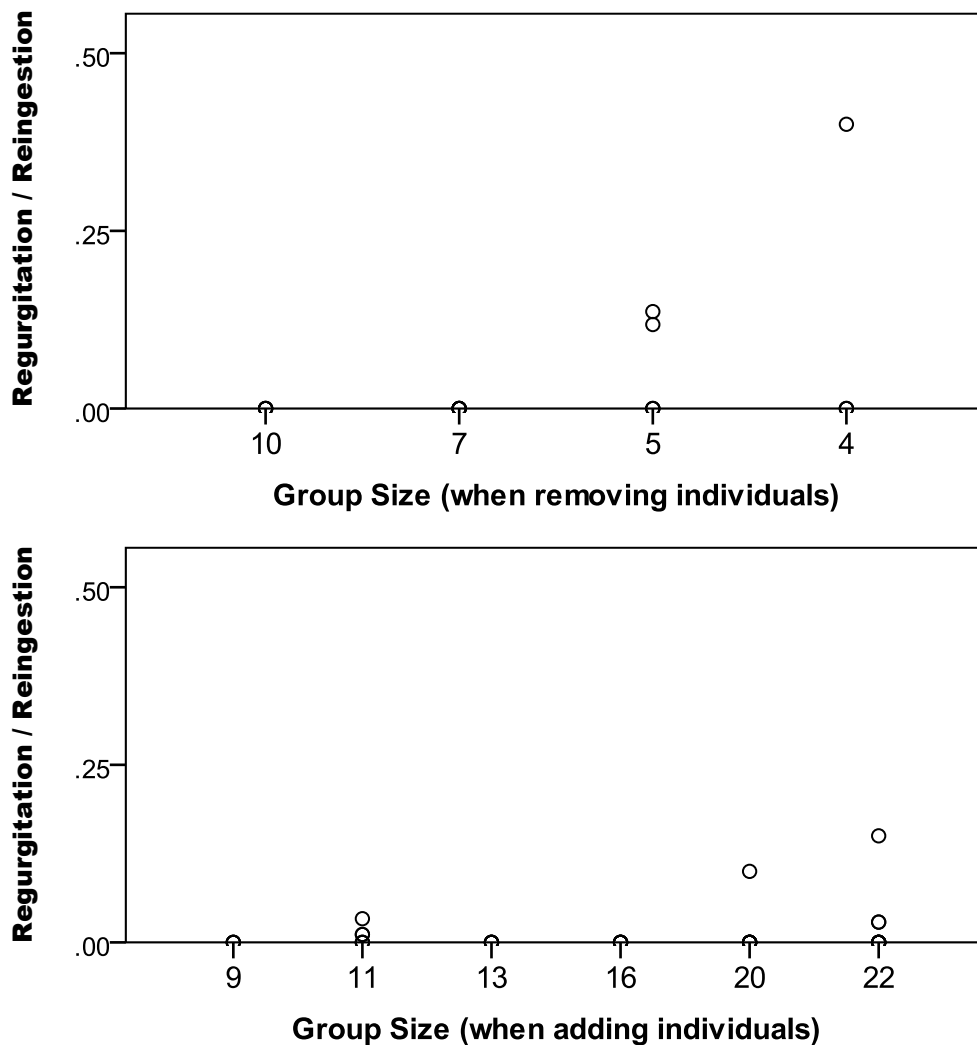


Figure 7.10. A comparison of group size versus regurgitation and reingestion rate per minute as individuals were removed from their original groups (top) and while individuals were added to the “super group” (bottom) for introduction purposes. The data represent only those who were known to exhibit R/R behaviours (i.e. Beekse Bergen group) and include a total of 21 individual averages for Individuals Removed and 44 for Individuals Added; see Appendix C3 for sample sizes per group size.

R/R did not significantly differ when individuals were removed (median = 0.029, $n = 5$) from original groups or added to the “super group” (median = 0.004, $n = 6$, Mann-Whitney U, $U = 9$, $z = -1.155$, $p = 0.248$, $r = -0.35$, see Figure 7.11).

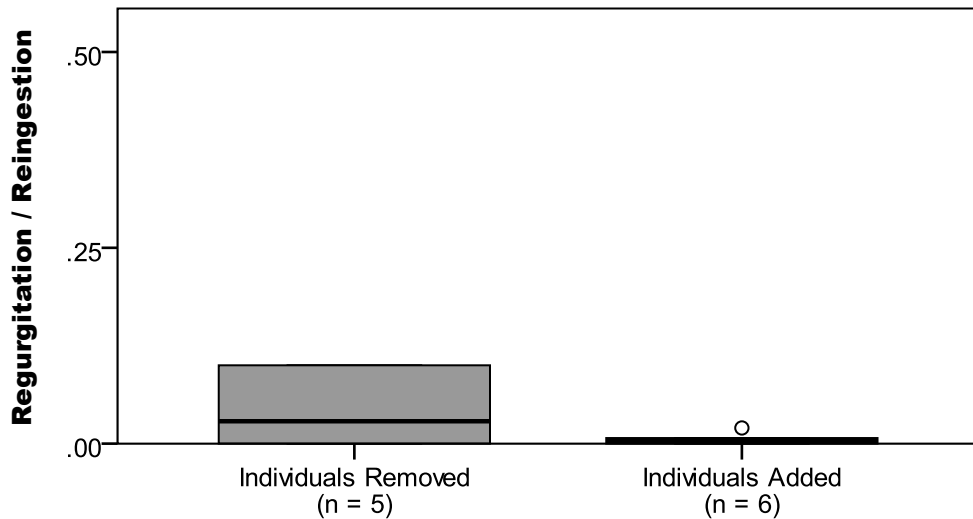


Figure 7.11. A comparison of the median and interquartile range (IQR) of the regurgitation and reingestion rate per minute comparing conditions during the introduction process when individuals were removed from their original group to when individuals were added to the “super group”. Data represents the 11 individuals who were known to exhibit R/R behaviours (i.e. Beekse Bergen group). Whiskers represent 5th and 95th percentiles. The outlier in the Individuals Added condition represents Lianne (0.02).

7.4.2.4 (D) ALLOGROOMING IN RELATION TO CHANGES IN GROUP SIZE

In accordance with the hypothesis, allogrooming increased as individuals were added to the “super group” and group size increased (Spearman’s correlation coefficient, $r = 0.33$, $p = 0.002$, $n = 91$), but did not decrease as individuals were removed and overall group size decreased (Spearman’s correlation coefficient, $r = -0.21$, $p = 0.91$, $n = 34$, see Figure 7.12). In accordance with the hypothesis, when examined overall (regardless of removal or addition of individuals) allogrooming increased as group size increased (Spearman’s correlation coefficient, $r = 0.256$, $p = 0.004$, $n = 125$, see Figure 7.12).

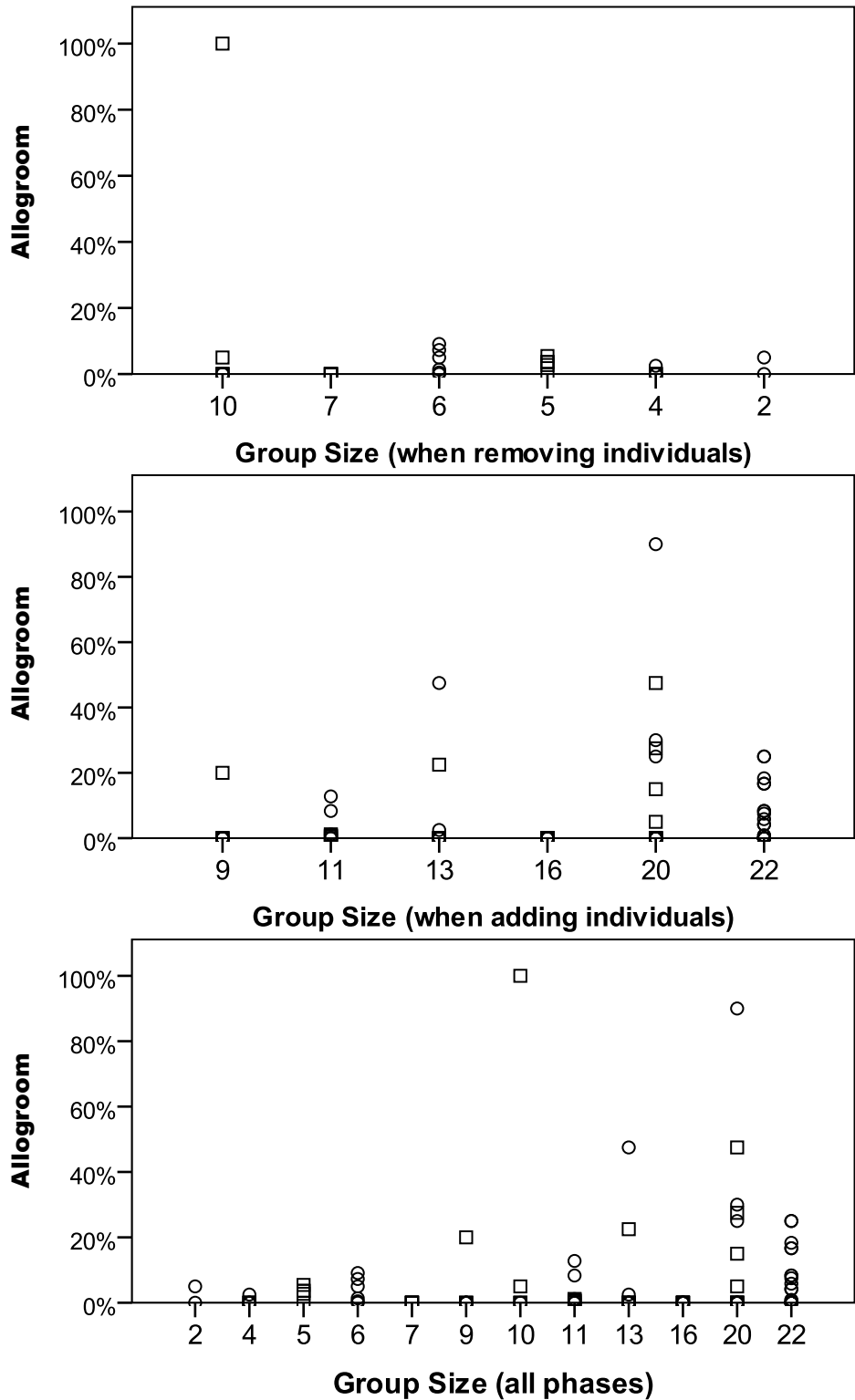


Figure 7.12. A comparison of group size versus estimated percentage of allogrooming as individuals were removed from their original groups (top), as individuals were added to the “super group” (middle), and throughout the introduction process: from Before Mix through the entire Integration phase (bottom). Circles represent data points for the Edinburgh group and squares represent values for the Beekse Bergen group. The data include a total of 34 individual averages when removing individuals, 91 when adding individuals, and 125 for the entire group size set; see Appendix C3 for sample sizes per group size.

Allogrooming did not significantly differ when individuals were removed (mean = 2.96, SE mean = 0.84, $n = 11$) from original groups or added to the “super group” (mean = 3.28, SE mean = 1.3, $n = 11$); Independent samples t-test, $t(20) = 0.284$, $p = 0.78$, see Figure 7.13).

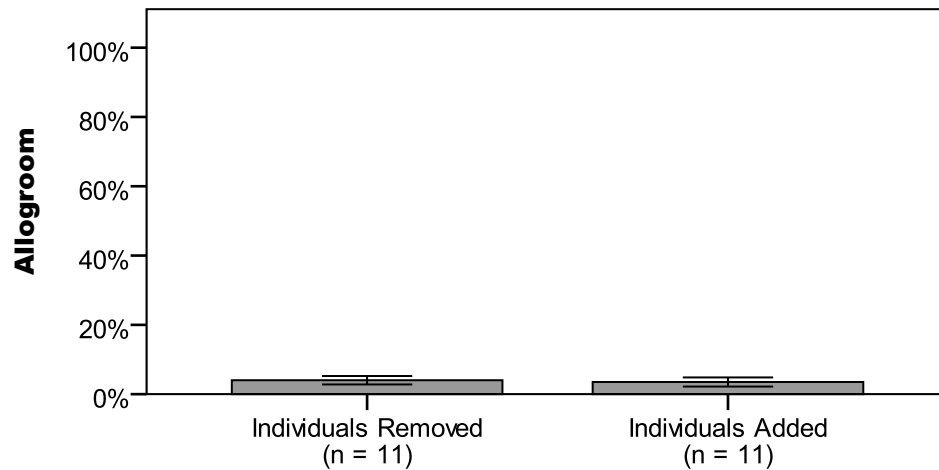


Figure 7.13. A comparison of the mean (+/- 1 SE) estimated percentage of time spent allogrooming during the introduction process when individuals were removed from their original group to when individuals were added to the “super group”.

7.4.3 ANALYSIS 3: AVAILABLE SPACE: NUMBER OF ROOMS

7.4.3.1 (A) SDBS IN RELATION TO NUMBER OF AVAILABLE ROOMS

Some, but not all SDBs significantly decreased when more rooms (excluding the outdoor enclosure) were available (see Figure 7.14). There was a significant difference in scratching across available rooms (Friedman’s two-way ANOVA, $\chi^2(2) = 8.17$, $p = 0.017$, $n = 12$). While scratching did not statistically differ from one (median = 0.39, $n = 12$), to two (median = 0.44, $n = 12$), rooms (Wilcoxon signed ranks test, $T = 41.0$, $r = 0.03$, $p = 0.87$), it decreased from two to three (median = 0.125, $n = 12$, $T = 12.0$, $r = -0.43$, $p = 0.03$, see Figure 7.14). Rubbing remained the same across all available rooms (Friedman’s two-way ANOVA, $\chi^2(2) = 3.17$, $p = 0.21$, $n = 12$). There was a significant difference in yawning across available rooms (Friedman’s two-way ANOVA, $\chi^2(2) = 11.13$, $p = 0.004$, $n = 12$). While yawning did not significantly differ from one to two rooms ($T = 46.0$, $r = 0.24$, $p = 0.25$), it decreased from two to three rooms ($T = 0.00$, $r = -0.51$, $p = 0.01$, see Figure 7.14): one room (median = 0.025, $n = 12$), two rooms (median = 0.05, $n = 12$), and three rooms (median = 0.00, $n = 12$).

To ensure the results were not confounded by density, the average number of individuals per room (based on total group members on the observation days) was compared. There was a significant difference in density across available rooms (Friedman's two-way ANOVA, $\chi^2(2) = 7.17, p = 0.028, n = 12$). Even though density was significantly higher in one room compared to two rooms (Wilcoxon signed ranks test, $T = 6.0, r = -0.53, p = 0.01$): one room (median = 8.15, $n = 12$) and two rooms (median = 5.40, $n = 12$), there was no difference in density between two and three rooms ($T = 52.0, r = 0.21, p = 0.31$, see Figure 7.15): three rooms (median = 6.08, $n = 12$). Since our significant results occurred when increasing from two to three rooms, density alone is insufficient to account for this change.

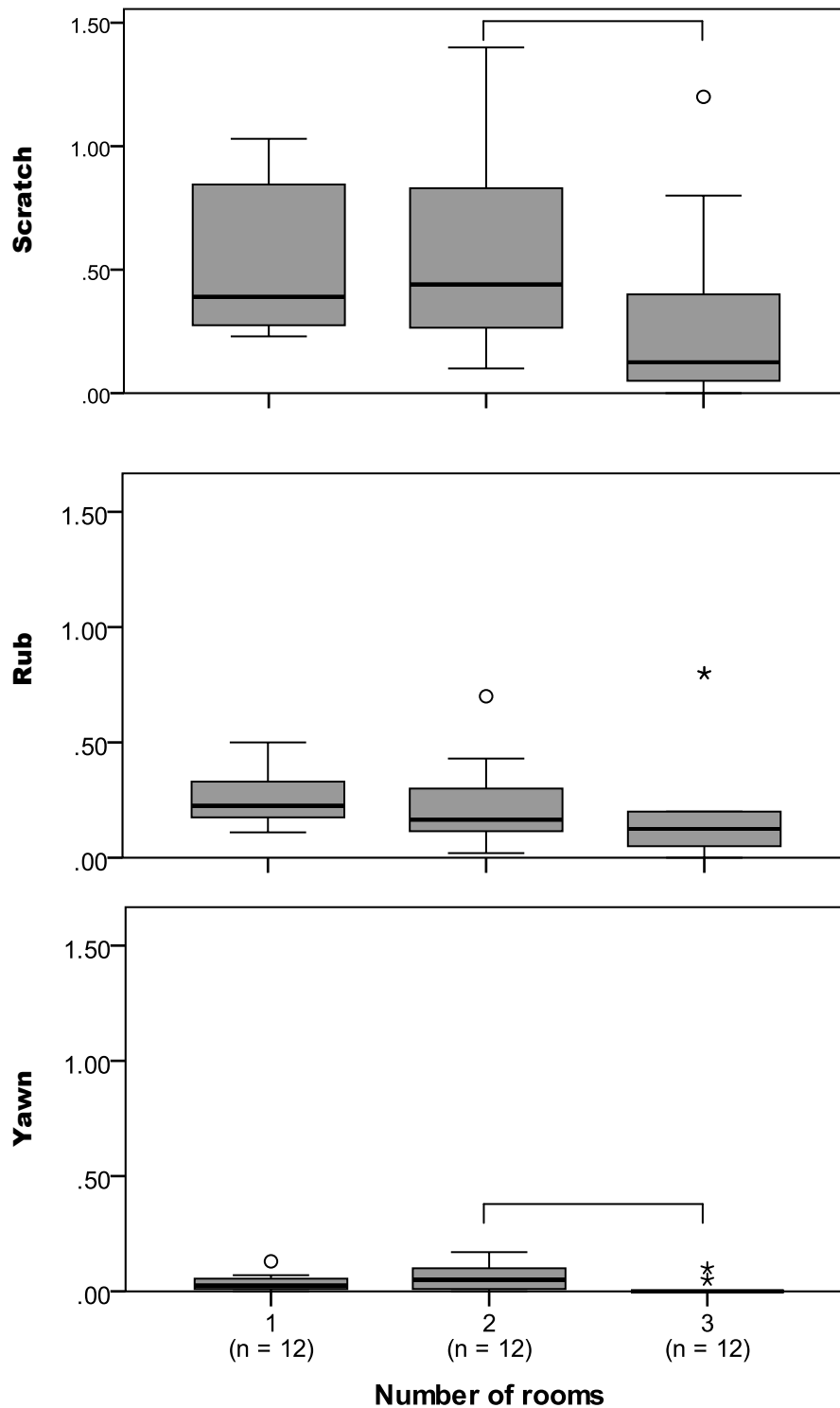


Figure 7.14. A comparison of the median and interquartile range (IQR) of SDB rates per minute (scratch, rub, and yawn) across the number of rooms in the enclosure where access was provided, not including the outdoor enclosure. Whiskers for represent 5th and 95th percentiles; circles and asterisk represent outliers; adjoining brackets highlight significant differences. The outliers represent: Scratch – three rooms: Cindy (1.2). Rub – two rooms: Liberius (0.70); three rooms: Cindy (0.80) and Emma (0.80). Yawn – one room: Liberius (0.13); three rooms: Liberius (0.10) and Lyndsey (0.05).

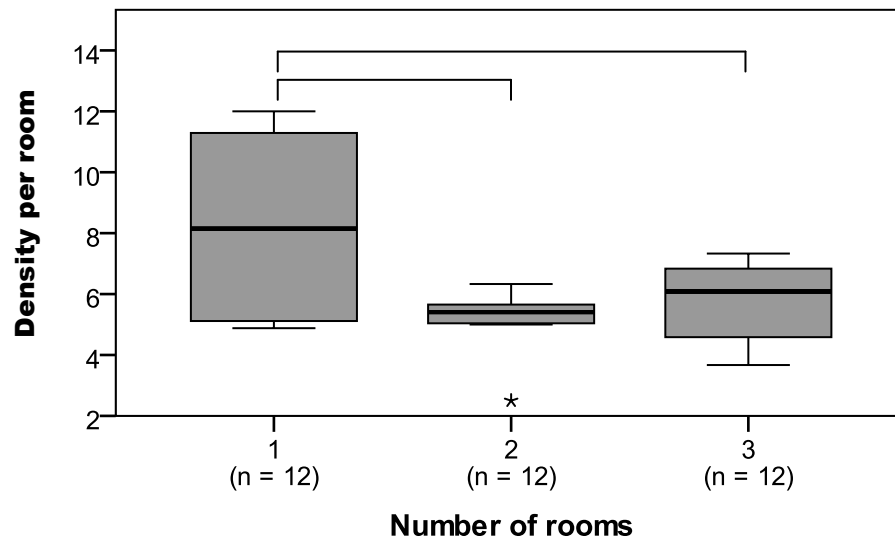


Figure 7.15. A comparison of the median and interquartile range (IQR) of the density per room. The average number of individuals per room for each number of accessible rooms. Whiskers for represent 5th and 95th percentiles; adjoining brackets highlight significant differences.

7.4.3.2 (B) R/R IN RELATION TO THE NUMBER OF AVAILABLE ROOMS

R/R remained constant and did not differ from one room (median = 0.05, mean = 0.08, SE mean = 0.38, $n = 12$), to two rooms (median = 0.00, mean = 0.03, SE mean = 0.17, $n = 12$, Wilcoxon signed rank test, $T = 3.0$, $r = -0.25$, $p = 0.22$, $n = 12$) or from two to three rooms (median = 0.00, mean = 0.02, SE mean = 0.15, $n = 12$, $T = 3.0$, $r = -0.15$, $p = 0.46$, see Figure 7.16).

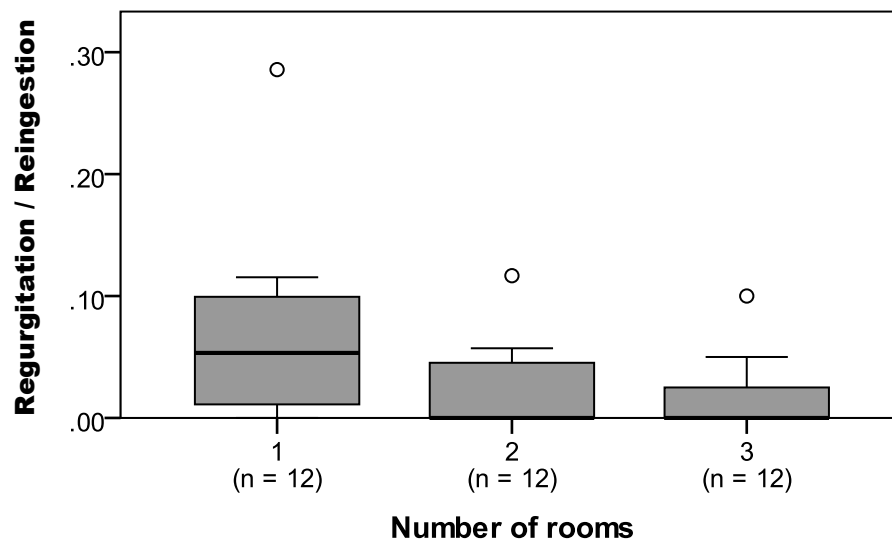


Figure 7.16. A comparison of the median and interquartile range (IQR) of the regurgitation and reingestion rate per minute across the number of rooms in the enclosure where access was provided, not including the outdoor enclosure. Whiskers for represent 5th and 95th percentiles; circles represent outlier. The outliers represent: one room: Lianne (0.29); two rooms: Sophie (0.12); three rooms: Sophie (0.10). Data represents only those who were known to exhibit R/R behaviours (i.e. the Beekse Bergen group) and those who were observed in all three conditions.

7.4.3.3 (C) ALLOGROOMING IN RELATION TO THE NUMBER OF AVAILABLE ROOMS

Allogrooming decreased as the number of accessible rooms increased from one to two rooms (Wilcoxon signed ranks test, $T = 8.0$, $r = -0.45$, $p = 0.03$), but not from two to three rooms ($T = 15.0$, $r = 0.19$, $p = 0.34$, see Figure 7.17): one room (median = 3.20, mean = 4.94, SE mean = 0.81, $n = 12$), two rooms (median = 0.00, mean = 0.82, SE mean = 0.49, $n = 12$), three rooms (median = 0.00, mean = 5.62, SE mean = 3.7954, $n = 12$).

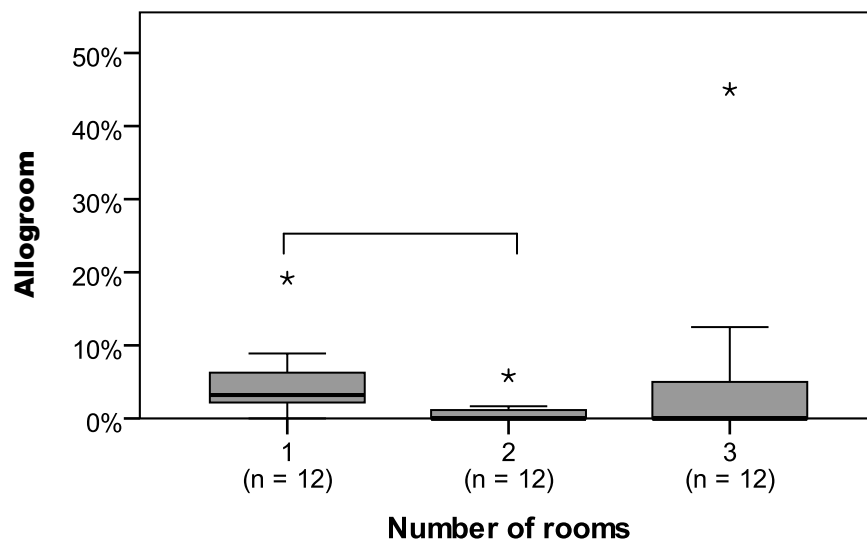


Figure 7.17. A comparison of the median and interquartile range (IQR) of the percentage of time spent allogrooming across the number of rooms in the enclosure where access was provided, not including the outdoor enclosure. Whiskers represent 5th and 95th percentiles; asterisks represent outliers; adjoining brackets highlight significant differences. The outliers represent: one room: Emma (19%); two rooms: Claus (6%); three rooms: Bram (45%).

7.4.4 ANALYSIS 4: AVAILABLE SPACE: SIZE

7.4.4.1 (A) SDBS IN RELATION TO SIZE OF AVAILABLE SPACE

Most SDB rates were not significantly different based on the size of the available space (see Figure 7.18). Yawning frequency was higher when space was restricted (median = 0.05, mean = 0.05, SE = 0.008, $n = 19$) than in higher space conditions (median = 0.00, mean = 0.02, SE = 0.01, $n = 19$; Wilcoxon signed ranks test, $T = 20$, $r = -0.46$, $p = 0.004$). All other SDBs remained constant: scratch (low: median = 0.38, mean = 0.47, SE = 0.05, $n = 19$; high: median = 0.30, mean = 0.39, SE = 0.10, $n = 19$; $T = 62$, $r = -0.22$, $p = 0.18$) and rub (low: median = 0.21, mean = 0.23, SE = 0.02, $n = 19$; high: median = 0.2, mean = 0.2, SE = 0.04, $n = 19$; $T = 61$, $r = -0.22$, $p = 0.18$).

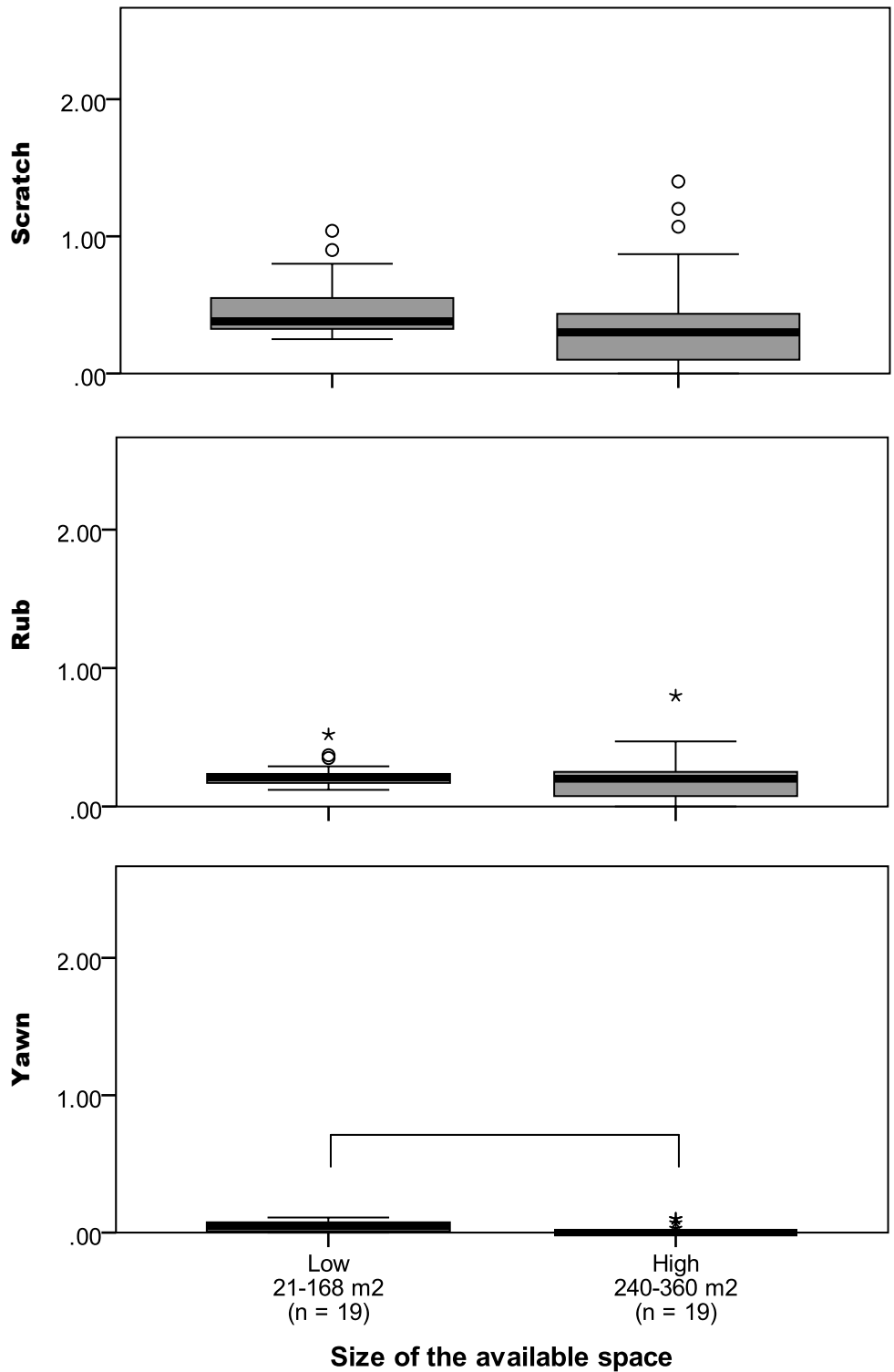


Figure 7.18. A comparison of the median and interquartile range (IQR) of SDB rates per minute (scratch, rub, and yawn) and the square metres of enclosure space where access was provided. Whiskers represent 5th and 95th percentiles; circles and asterisk show outliers; adjoining brackets highlight significant differences. The outliers represent: Scratch – low: Cindy (1.04) and Lyndsey (0.90); high: Lyndsey (1.07), Cindy (1.2), and Kilimi (1.4). Rub – low: Lyndsey (0.35), Qafzeh (0.37), and Liberius (0.52); high: Cindy (0.80). Yawn – high: Lyndsey (0.03), Emma (0.07), Liberius (0.10), and Louis (0.10).

7.4.4.2 (B) R/R IN RELATION TO SIZE OF AVAILABLE SPACE

R/R did not decrease as the size of the available space increased and group density decreased (median = 0, mean = 0.01, SE = 0.01, $n = 9$) compared to low space conditions (median = 0.27, mean = 0.43, SE = 0.02, $n = 9$) (Wilcoxon signed ranks test, $T = 2$, $r = -0.35$, $p = 0.14$, see Figure 7.19): low space and high space.

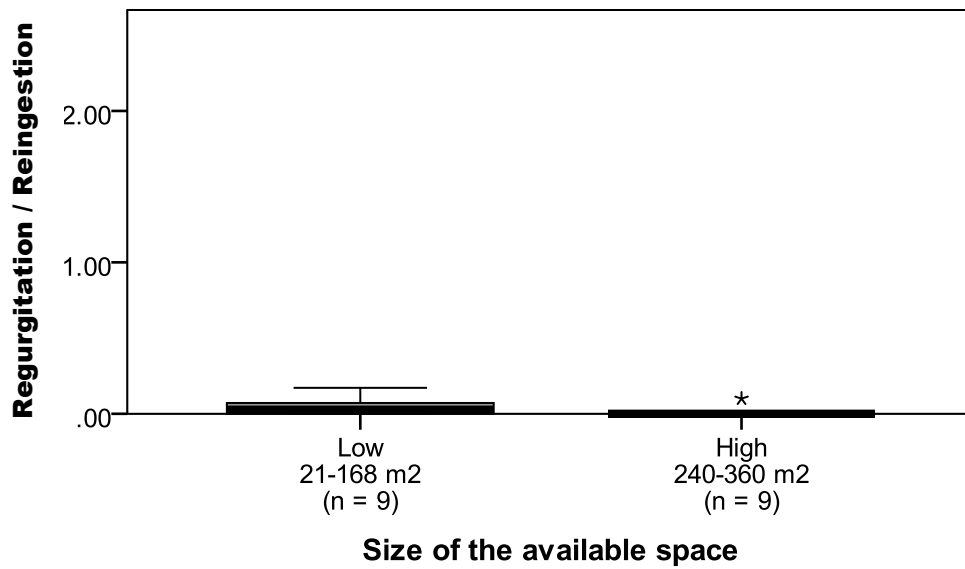


Figure 7.19. A comparison of the median and interquartile range (IQR) of the regurgitation and reingestion rate per minute and the square metres of enclosure space where access was provided. Data represents only those who were known to exhibit R/R behaviours (i.e. the Beekse Bergen group) and those who were observed in all three conditions. Whiskers represent 5th and 95th percentiles; asterisk show outliers. The outlier represents: High: Sophie (0.10).

7.4.4.3 (C) ALLOGROOMING IN RELATION TO SIZE OF AVAILABLE SPACE

Allogrooming did not decrease as the size of the available space decreased (Wilcoxon signed ranks test, $T = 74.5$, $r = -0.01$, $p = 0.93$, see Figure 7.20): low space (median = 2.5, mean = 3.83, SE mean = 1.03, $n = 19$) high space (median = 0, mean = 4.78, SE mean = 1.94, $n = 19$).

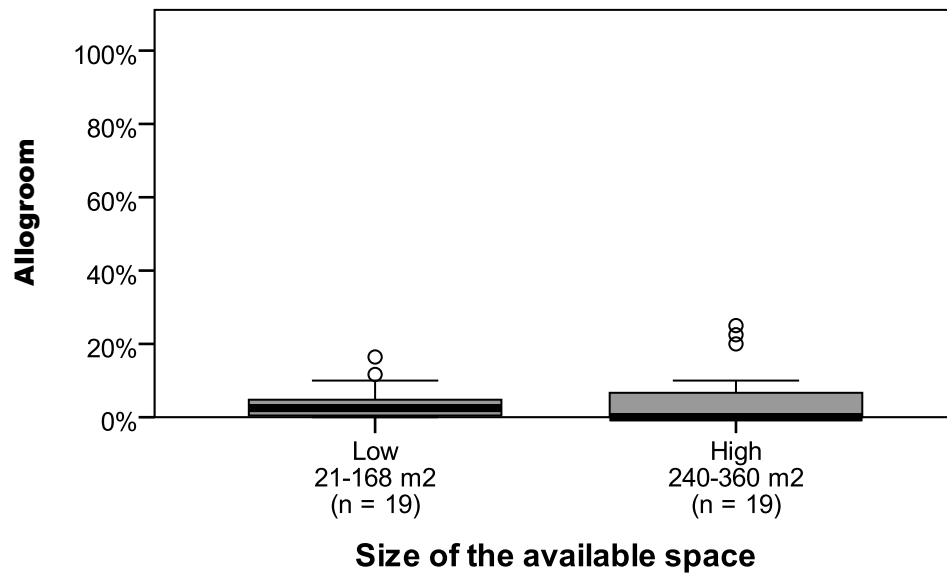


Figure 7.20. A comparison of the median and interquartile range (IQR) of the estimated percentage of time spent allogrooming and the square metres of enclosure space where access was provided. Data represent only those who were observed in both conditions. Whiskers represent 5th and 95th percentiles; circles and asterisk show outliers. The outliers represent: Low: Edith (11.67%) and Emma (16.43%). High: Paul (20%), Bram (22.5%), and Edith (25%).

7.4.5 ANALYSIS 5: R/R GROUP TRANSFER

(a) Abnormal behaviours did not transfer across groups. The Edinburgh group never exhibited R/R during the observation sessions.

7.4.6 ANALYSIS 6: ALLOGROOMING: RELATIONSHIPS BETWEEN RANK, SEX, AND KIN

All individuals except for one (Cindy from the Edinburgh group) were observed allogrooming others during observation periods over the course of the study: Before Mix through Integration. Allogrooming occurred within the two groups an estimated 4.3% of the time.

7.4.6.1 (A) GROOMING BY RANK

Rank was positively correlated with performing allogrooming (Spearman's correlation coefficient, $r = -0.472$, $p = 0.03$, $n = 22$) whereas rank was not significantly correlated with receiving grooming (Spearman's correlation coefficient, $r = -0.014$, $p = 0.95$, $n = 22$, see Figure 7.21). The higher the rank the more allogrooming (giving) occurs. It is important to note that the negative r value reflects that opposite nature of the ranking order, where 1 is highest as opposed to 11, therefore the correlation is considered positive.

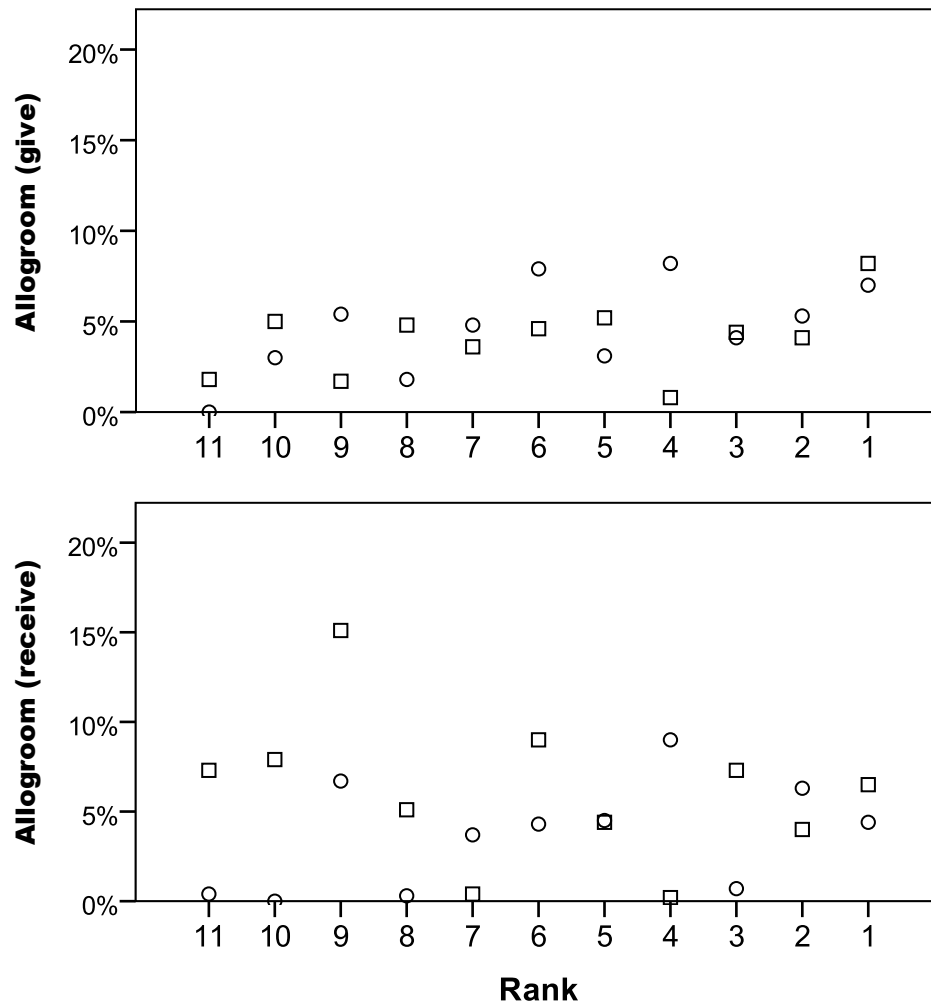


Figure 7.21. A comparison of the estimated percentage of time spent allogrooming – give (top) and receive (bottom) versus rank (see Table 2.2). With each group consisting of a 1-11 rank order where 1 is the highest ranking and 11 is the lowest ranking, there are two data points for each rank ($n = 22$). Circles represent data points for the Edinburgh group and squares represent values for the Beekse Bergen group.

7.4.6.2 (B) FEMALE AND MALE PATTERNS IN ALLOGROOMING

For those who participated in allogrooming others, there was no difference in females grooming different ranks (Independent samples t-test, $t(18) = -0.30$, $p = 0.98$, see Figure 7.22): high-ranking (mean = 39.65, SE mean = 7.95, $n = 10$) and low-ranking individuals (mean = 39.29, SE mean = 8.76, $n = 10$).

There was no difference in males grooming different ranks (Independent samples t-test, $t(20) = -0.86$, $p = 0.40$, see Figure 7.22): high-ranking (mean = 40.78, SE mean = 8.93, $n = 11$) and low-ranking individuals (mean = 31.24, SE mean = 6.55, $n = 11$).

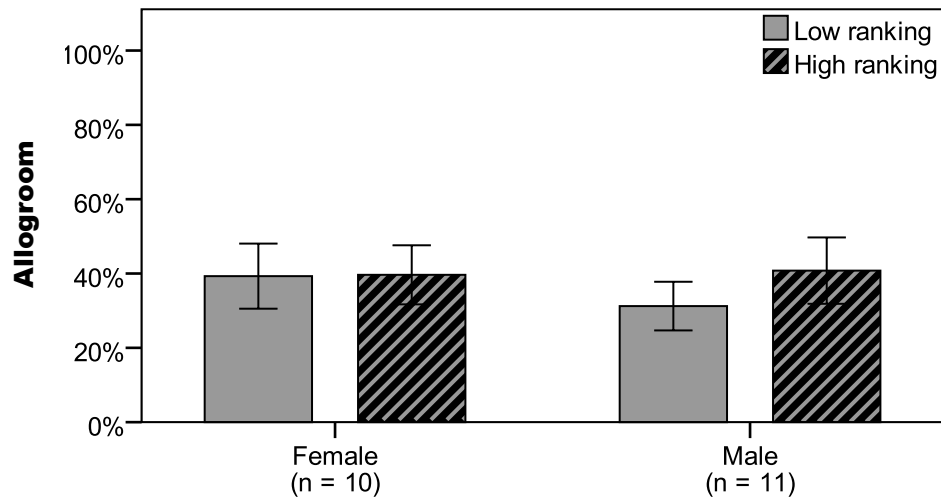


Figure 7.22. A comparison of the mean (± 1 SE) estimated percentage of time spent allogrooming high-ranking versus low-ranking individuals (as a percentage of the overall time spent grooming), separated by sex.

When examined before and after the groups merged, there was no difference in female grooming based on rank of the recipient (Wilcoxon signed ranks test, $T = 1$, $r = -0.24$, $p = 0.28$, see Figure 7.23): low-ranking (median = 0, mean = 8.18, SE mean = 8.18, $n = 10$) and high-ranking (median = 0, mean = 21.8, SE mean = 13.15, $n = 10$) individuals. Nor was there a difference in the Integration phase for females grooming different ranks (Wilcoxon signed ranks test ($T = 27$, $r = -0.01$, $p = 0.96$): low-ranking (median = 40.01, mean = 36.11, SE mean = 9.98, $n = 10$) and high-ranking (median = 28, mean = 35.5, SE mean = 8.33, $n = 10$) individuals. There was no difference in the Before Mix phase for males grooming different ranks (Wilcoxon signed ranks test, $T = 1.5$, $r = 0$, $p > 0.05$): low-ranking (median = 0, mean = 9.09, SE mean = 9.09, $n = 11$) and high-ranking (median = 0, mean = 9.09, SE mean = 9.09, $n = 11$) individuals. Nor was there a difference in the Integration phase for males grooming different ranks (Wilcoxon signed ranks test, $T = 37$, $r = 0.08$, $p = 0.72$): low-ranking (median = 34, mean = 41.29, SE mean = 9.56, $n = 11$) and high-ranking (median = 32, mean = 34.18, SE mean = 10.17, $n = 11$) individuals.

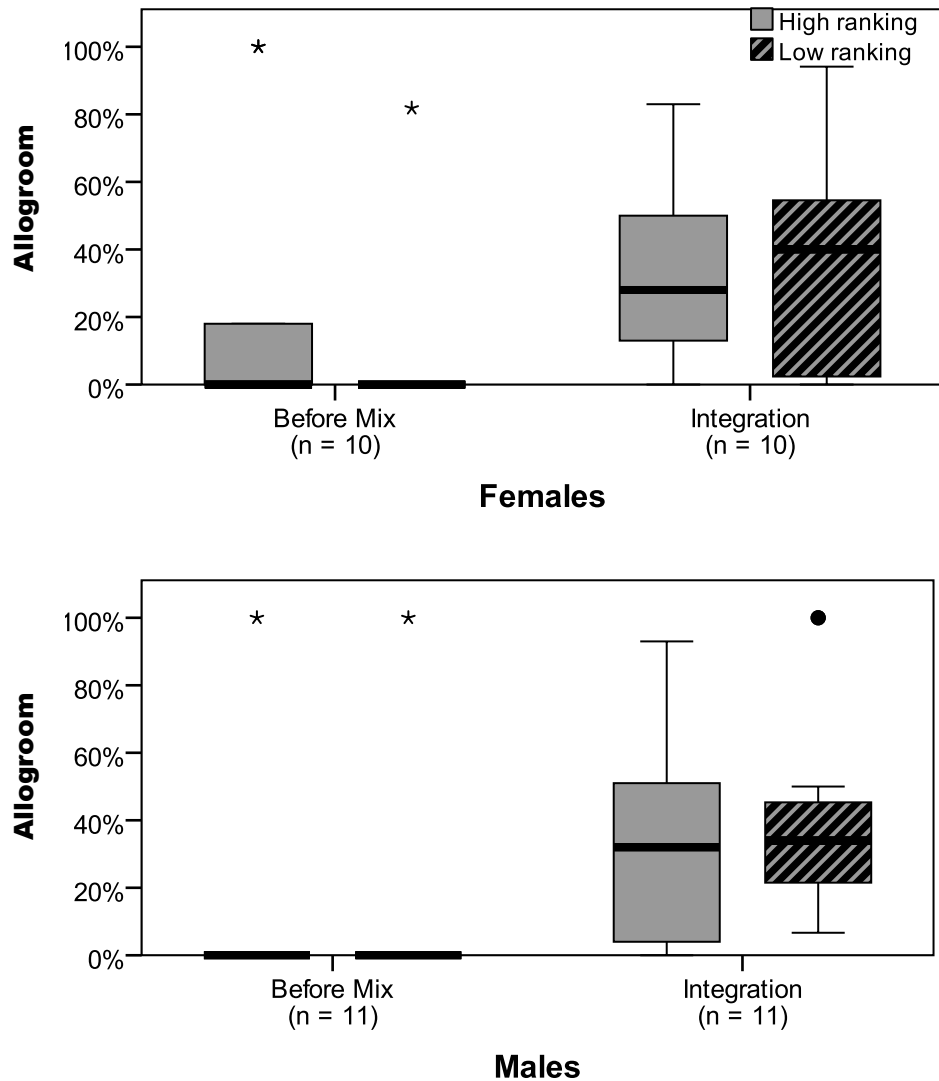


Figure 7.23. A comparison of the median and interquartile range (IQR) of the estimated percentage of time spent allogrooming high-ranking versus low-ranking individuals (as a percentage of the overall time spent grooming), before and after the two groups merged. Graphs are separated by sex: females (top) and males (bottom). Whiskers represent 5th and 95th percentiles; circle and asterisk show outliers. The outliers represent females: Before Mix – high ranking, Eva (100%) and Pearl (100%), low ranking, Heleen (81.82%); males: Before Mix – high ranking, Liberius (100%), low ranking, Paul (100%); Integration – low ranking, Kindia (100%) and Paul (100%).

For all chimpanzees in the group there was no difference in the estimated percentage of time spent grooming males (Independent samples t-test, $t(19) = 0.548$, $p = 0.59$, see Figure 7.24): males (mean = 46.81, SE mean = 7.8, $n = 11$) and females (mean = 53.3, SE mean = 9.0, $n = 11$).

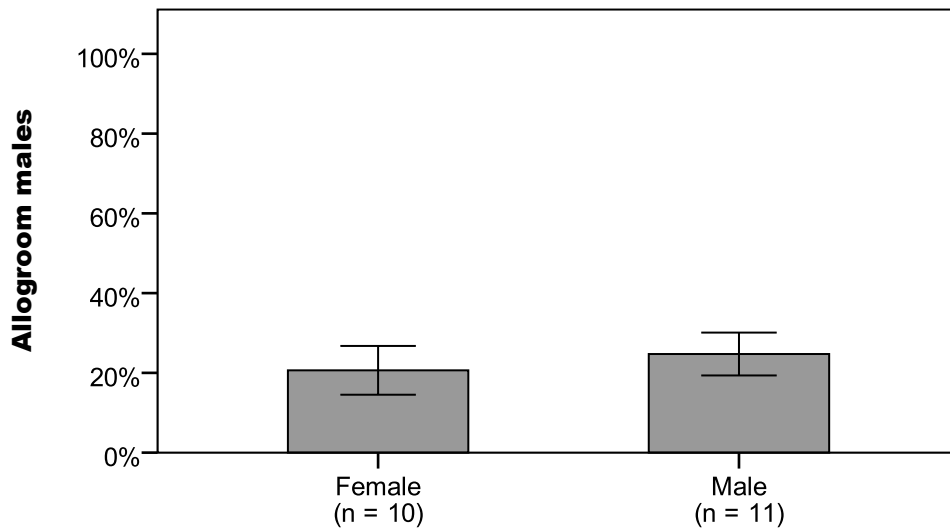


Figure 7.24. A comparison of the mean (\pm 1 SE) estimated percentage of time spent allogrooming males (as a percentage of the overall time spent grooming), separated by sex.

There was no statistical difference for either sex between the grooming of in-group males (Mann-Whitney U-test, $U = 53.5$, $z = -0.11$, $p = 0.92$, $r = 0.02$, see Figure 7.25): males (median = 58, mean = 44.91, SE mean = 11.39, $n = 11$) and females (median = 48.4, mean = 48.51, SE mean = 10.54, $n = 10$).

Nor was there a difference for either sex in grooming out-group males (Mann-Whitney U-test, $U = 38.5$, $z = -1.91$, $p = 0.056$, $r = -0.42$, see Figure 7.24): males (median = 0, mean = 0, SE mean = 0, $n = 11$) and females (median = 0, mean = 25.55, SE mean = 13.56, $n = 10$).

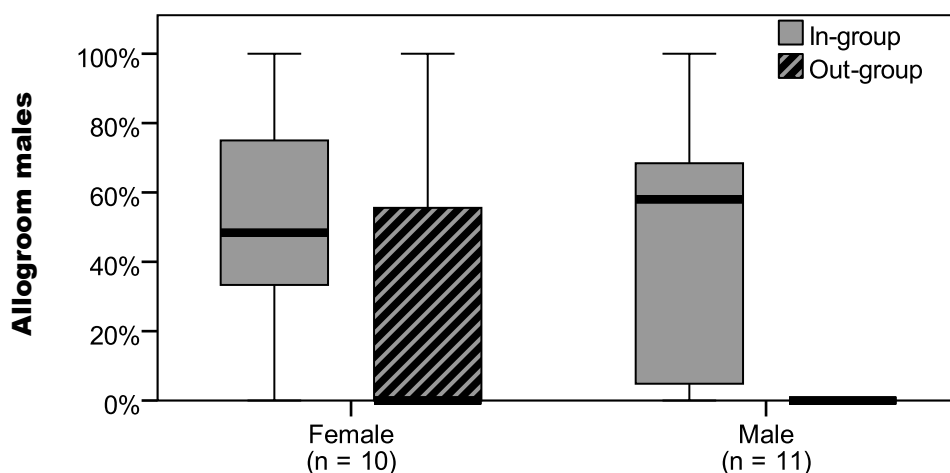


Figure 7.25. A comparison of the median and interquartile range (IQR) of the estimated percentage of time spent allogrooming in-group versus out-group individuals (as a percentage of the overall time spent grooming), separated by sex. Whiskers represent 5th and 95th percentiles.

When examined before and after the groups merged, there was still no significant difference between the sexes on grooming males before the merge (Mann-Whitney U test, $U = 49.5$, $z = -0.52$, $p = 0.60$, $r = -0.11$): males (median = 0, mean = 18.18, SE mean = 12.2, $n = 11$) and females (median = 0, mean = 21.82, SE mean = 13.15, $n = 10$). Nor was there a difference after the merge (Mann-Whitney U test, $U = 45.5$, $z = -0.67$, $p = 0.50$, $r = -0.15$): males (median = 56.25, mean = 40.80, SE mean = 10.15, $n = 11$) and females (median = 48.18, mean = 51.54, SE mean = 10.15, $n = 10$). Nor was there a difference between the Before Mix and Integration phases on male grooming for each sex: males (Wilcoxon signed ranks test, $T = 27$, $r = 0.27$, $p = 0.21$) or females ($T = 37$, $r = 0.38$, $p = 0.09$).

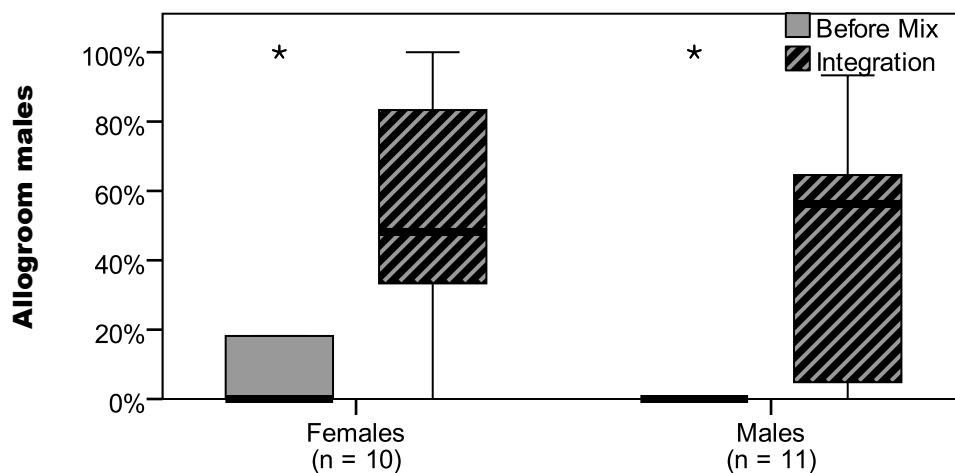


Figure 7.26. A comparison of the median and interquartile range (IQR) of the estimated percentage of time spent allogrooming males (as a percentage of the overall time spent grooming), before and after the two groups merged, separated by sex. Whiskers represent 5th and 95th percentiles; asterisk show outliers. The outliers represent Before Mix: females – Pearl (100%) and Eva (100%); males – Claus (100%) and Frek (100%).

7.4.7 ANALYSIS 7: ALLOGROOMING: IN-GROUP/OUT-GROUP

When all individuals from the Edinburgh and Beekse Bergen groups had the chance to mix socially (i.e. be in the same enclosure area) during the Integration phase, they chose to mix an estimated 48.7% of the time and allogroomed an estimated 5.2%, regardless of who was groomed.

7.4.7.1 (A) ALLOGROOMING DIFFERENCES BETWEEN IN-GROUP AND OUT-GROUP

In accordance with the hypothesis, the chimpanzees groomed in-group individuals (median = 100, mean = 81.99, SE mean = 6.8, $n = 21$) significantly more than they groomed out-group (median = 0.00, mean =

13.46, SE mean = 5.62, $n = 21$) individuals (Wilcoxon signed-rank test, $T = 9$, $r = -0.79$, $p < 0.001$, see

Figure 7.27).

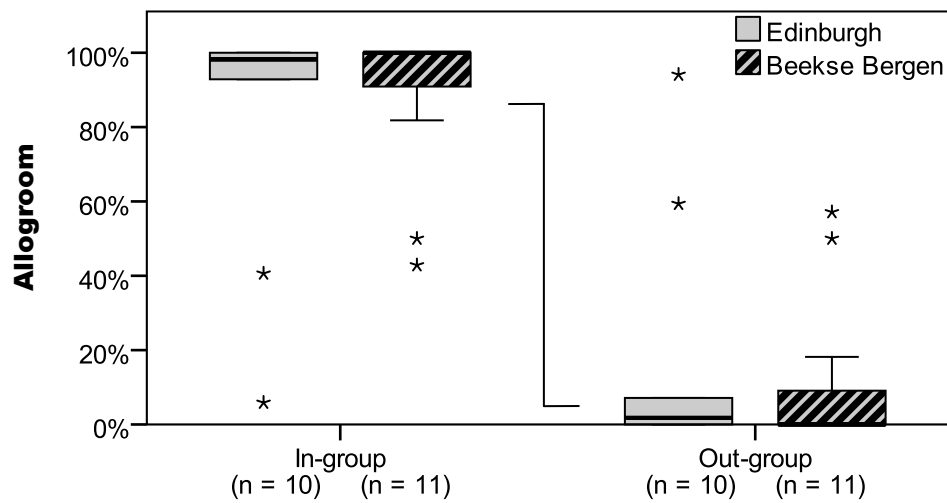


Figure 7.27. A comparison of the median and interquartile range (IQR) of the estimated percentage of total grooming time spent allogrooming familiar versus unfamiliar chimpanzees throughout the Integration phase. Cindy was excluded from the data set due to zero allogrooming data points (Edinburgh $n = 10$; Beekse Bergen $n = 11$). Whiskers represent 5th and 95th percentiles; adjoining brackets highlight significant differences; circles and asterisk show outliers. The outliers for Edinburgh In-group are Kilimi (5.88) and Louis (40.63); Beekse Bergen In-group are Sophie (42.86) and Lianne (50.0). The outliers for Edinburgh Out-group are Louis (59.38) and Kilimi (94.12); Beekse Bergen Out-group are Lianne (50.0) and Sophie (57.14).

Allogrooming of out-group individuals did not increase over time during the Integration phase

(Wilcoxon signed ranks test, $T = 5$, $r = 0.23$, $p = 0.28$, see Figure 7.28): Initial Integration (median = 0,

mean = 5.08, SE mean = 4.76, $n = 21$) and Follow-up Integration (median = 0, mean = 14.29, SE mean =

7.8, $n = 21$). Similar results were found for in-group individuals where allogrooming did not increase

over time during the Integration phase (Wilcoxon signed ranks test, $T = 20$, $r = 0.07$, $p = 0.76$, see Figure

7.28): Initial Integration (median = 100, mean = 61.59, SE mean = 10.8, $n = 21$) and Follow-up Integration

(median = 100, mean = 61.9, SE mean = 10.86, $n = 21$).

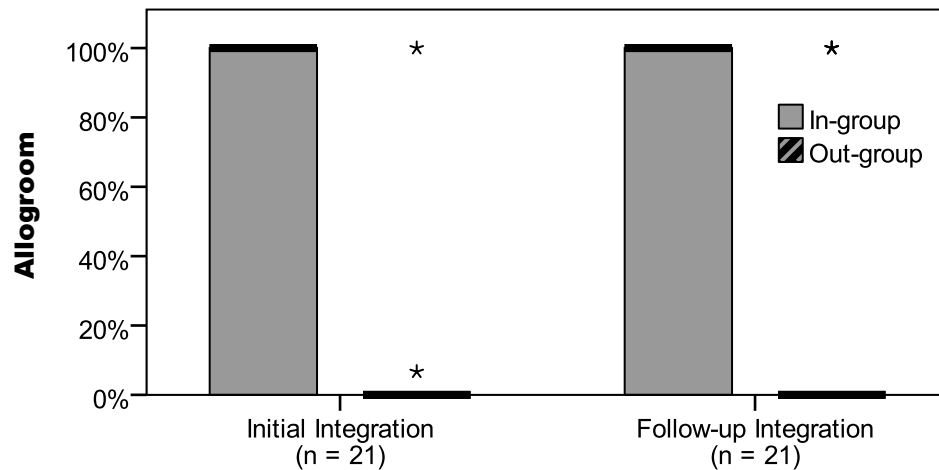


Figure 7.28. A comparison of the median and interquartile range (IQR) of the estimated percentage of time spent allogrooming in-group versus out-group individuals during Initial Integration and Follow-up Integration (see Table 7.1). Whiskers represent 5th and 95th percentiles; asterisk show outliers. The outliers for Initial Integration out-group are Lianne (6.67%) and Edith (100%); Follow-up Integration out-group are Kilimi (100%), Kindia (100%), and Edith (100%).

7.4.7.2 (B) SEX DIFFERENCES BETWEEN IN-GROUP AND OUT-GROUP

During integration, females (median = 0.0, mean = 18.37, SE mean = 9.87, $n = 10$) did not groom out-group individuals more than males (median = 0.0, mean = 7.3, SE mean = 5.3, $n = 11$, Mann Whitney U-test, $U = 48$, $z = -0.56$, $p = 0.57$, $r = -0.12$, see Figure 7.29).

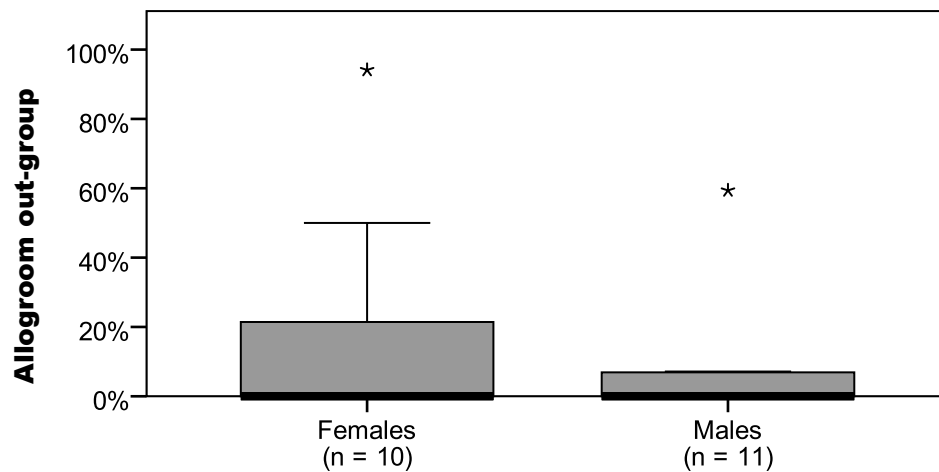


Figure 7.29. A comparison of the median and interquartile range (IQR) of the estimated percentage of time spent allogrooming out-group individuals. Whiskers represent 5th and 95th percentiles; asterisk show outliers. The outliers are Kilimi (94.12%) and Louis (59.38%).

7.4.7.3 (C) KIN WITHIN GROUP: OVERALL

Those with kin in their group (raised with kin: mean = 4.74, SE mean = 0.83, $n = 10$; not raised as kin (mean = 4.3, SE mean = 0.48, $n = 7$), did not groom more overall than those without kin (mean = 2.96, SE mean = 0.79, $n = 5$, One-way ANOVA, $F(2, 19) = 1.16$, $p = 0.33$, see Figure 7.30)⁷. In accordance with the hypothesis, those with kin in their group groomed them at a higher percentage after the two groups merged (Wilcoxon signed ranks test, $T = 28$, $r = 0.79$, $p = 0.02$, see Figure 7.31): Before Mix (all scores = 0, $n = 9$) and Integration (median = 21.05, $n = 9$).

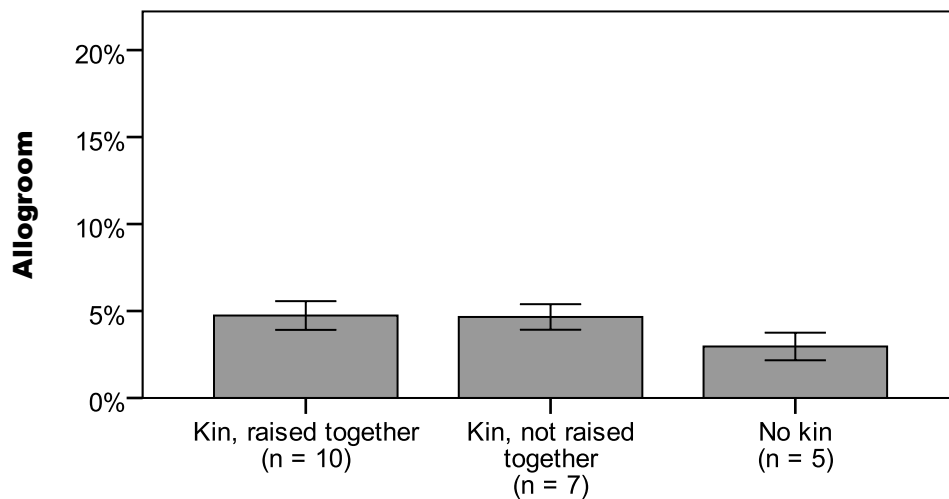


Figure 7.30. A comparison of the mean (± 1 SE) estimated percentage of time spent allogrooming for all chimpanzees based on kin status.

⁷ The same pattern was revealed when those who had kin in the group who were not raised with them (or kin status was only identified through DNA testing) were separately analysed as a part of both the raised together and no kin groups.

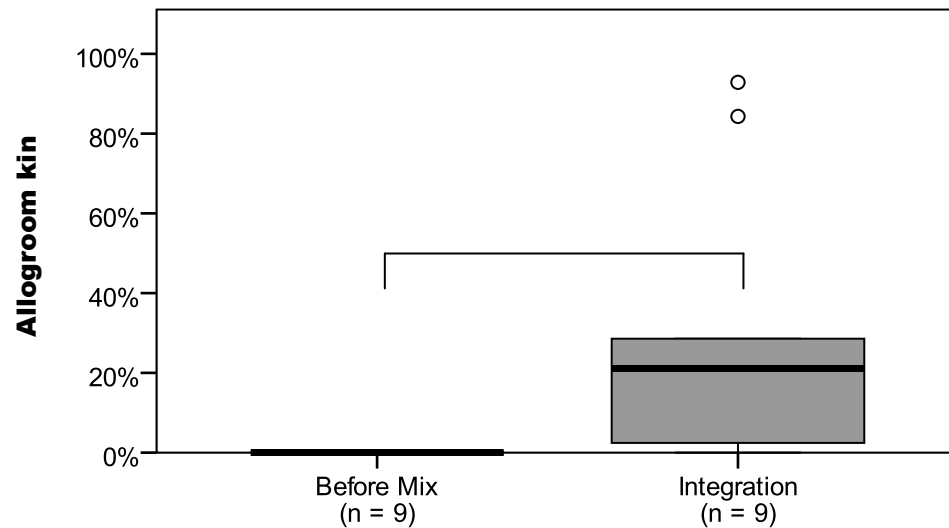


Figure 7.31. A comparison of the median and interquartile range (IQR) of estimated percentage of time spent allogrooming kin (of those who had been raised with kin) before and after the two groups merged. Whiskers represent 5th and 95th percentiles; adjoining bracket highlights a significant difference; circles show outliers. The outliers are Lyndsey (84%) and Kindia (93%).

7.4.8 SUMMARY OF RESULTS

When examining the phases of the introduction process, we can conclude that rub rates decreased from the Baseline phase until the creation of the “super group” began in the Mix phase and then decreased again when all individuals were together in the Integration phase to a rate lower than Baseline levels. Yawning also significantly decreased after the Mix phase when all 22 chimpanzees were together. At the same time, scratch and R/R rates remained constant across the phases. The estimated percentage of time spent allogrooming remained constant.

In examining the impact of integration, rub rates and R/R were found to decrease over time: Rub decreased from Baseline to Initial Integration and decreased again during the Follow-up Integration phase while R/R became statistically non-existent during Initial and Follow-up Integration. However, scratch and yawn rates did not differ over time. The decrease in the undesirable behaviour of R/R over time was a huge improvement for this group as it was a topic of great concern with their previous keepers (W. Bruijn, personal communication, 2010). With the many changes the group underwent to become a part of the Edinburgh group (e.g. international transport and new housing, keepers, schedules, diets, group members, etc.), determining the factors that played a role in the decrease would be difficult.

Scratch, rub, and yawn rates increased as group size decreased, but remained constant as group size increased. When examining sub groups as individuals were removed or added, rub occurred at higher rates when individuals were removed compared to when added, whereas scratch, yawn, and R/R rates and the estimated percentage of time spent allogrooming remained constant. R/R remained constant regardless of the direction of change in group size both during the changes. Allogrooming on the other hand, remained constant as individuals were removed from their groups, but increased as individuals were added.

When looking at available space while controlling for density, scratching and yawning decreased as the number of available rooms increased whereas only yawning decreased as the amount of available space (square metres) increased. Rubbing and R/R rates remained constant as both the number of rooms and amount of space changed. Allogrooming decreased when the number of rooms increased from one to two, however, average density also decreased when rooms increased from one to two.

When individual(s) from both groups chose to be in the same enclosure area, the estimated percentage of time spent allogrooming was highest with in-group chimpanzees. There was no difference between in- and out-group grooming between sexes nor were there any changes in the percentage of time spent grooming in- versus out-group members as the chimpanzees spent more time within the Integration phase.

There was no difference in the grooming of males by either sex regardless of whether or not the males were in- or out-group or whether it was before or after the groups merged. Overall grooming percentages were not influenced by the status of having kin in the group. Rank of the recipient had no bearing on allogrooming by either sex, regardless of whether or not the two groups had merged, but was positively correlated with grooming in that those who were higher ranking groomed more than those who were lower ranking.

7.5 DISCUSSION

7.5.1 INTRODUCTION PROCESS

Given the previous research on self-directed behaviours as behavioural indicators of wellbeing (Captive studies: Aureli & de Waal, 1997; Baker & Aureli, 1997; Leavens et al., 2001; Troisi, 2002; Field studies: Itakura, 1993; Castles et al., 1999; Kutsukake, 2003a; Hockings, 2007), and the tense nature of chimpanzee introductions (Seres et al., 2001), it was expected that scratch, rub, and yawn rates would increase as each subsequent step in the introduction process involved more uncertainty and potential for aggression than the previous one. We also predicted increased R/R as a potentially adaptive response to the stressors of captivity (Lukas, 1999) or due to spreading via social learning (Hook et al., 2002). Contrary to expectations, no changes occurred for scratch and R/R rates or for the estimated percentage of time spent allogrooming. Even though the introduction process was a successful and relatively quick one with no major injuries, after observing the process it would be inappropriate to suggest that the lack of change amongst scratch and R/R rates indicated that events were not viewed as uncertain or potentially stressful for the chimpanzees. Perhaps, as Leavens et al. (2001) proposed, rubbing has a different motivational drive than other SDBs. Previous studies (Aureli & de Waal, 1997; Baker & Aureli, 1997) suggested that scratching is linked to social changes that have the potential to produce negative outcomes. Since rubbing rates increased during the Mix phase when scratching did not change, it might indicate that the situation is viewed as uncertain (in that they do not know how to behave), but not necessarily a negatively valenced context, predictive of a negative outcome. Many of the changes that occurred were new to the chimpanzees; the most recent addition to the Edinburgh group was the birth of Liberius in 1999 and everything about the enclosure, including the care staff, was new to the Beekse Bergen group. As a result, the function of rubbing might be linked to uncertain or potentially stressful and frustrating changes that do not (or are not known to) have the potential to produce negative outcomes.

The peak of rubbing during the Mix condition coincided with changes in group structure; individuals were separated from the group members they lived with for years and were placed in an environment where they were joined by an increasing number of familiar (in-group) and unfamiliar (out-group)

individuals. It was a necessary part of the introduction process, but potentially stressful nonetheless. The drop in rubbing behaviour when the two groups merged supports the potential function of the behaviour. Even though each chimpanzee was faced with establishing where they fit (rank) within the group, it was a familiar challenge that a chimpanzee in any group has encountered. The unfamiliar nature of the introduction process was over and while most behaviours tested did not change during the Integration phase (from the first three weeks – Initial Integration, to the last three weeks – Follow-up Integration), rubbing rates continued to decrease within the Integration phase.

7.5.2 CHANGES IN GROUP SIZE

The Mix category, when the chimpanzees from the two groups were merged into one, prompted the highest rates of rubbing across the phases of the introduction process. Within that phase the chimpanzees experienced individuals being removed and added to their groups. In response to an uncertain and stressful event such as the removal of an individual from a group or the addition of a new one, we expected changes in behaviour. Rubbing rates were higher when individuals were removed compared to when individuals were added. In contrast, Scratch, yawn, R/R rates, and the estimated percentage of time spent allogrooming, remained constant.

It could be argued that the removal of your own group members is more of an unfamiliar and unknown factor for those who have not been apart for years than it is to have new individuals added to your group along with familiar faces. Although Budongo Trail was designed to allow for constantly changing group compositions within the dynamic chimpanzee fission-fusion activities, free access to find others was not always possible during the introduction process. Overall, this result falls in line with previous literature and anecdotes suggesting that the departure of an individual, whether temporarily or permanently through death or zoo relocation, can be a stressful event for members of that animal's group (Box, 1984; Norcross & Newman, 1999; Peel et al., 2005; Anderson, 2011; Sarah Gregory, personal communication, 2010). The higher rate of rubbing when individuals were removed (an unfamiliar situation) compared to when individuals were added (a partly unfamiliar situation where they meet new chimpanzees and are reunited with familiar ones) supports the previously proposed function of the behaviour.

Further examination of the changes in group size while individuals were removed and added indicated that SDBs for the group increased as individuals were removed but not as they were added, although in both cases total group size changed. Additionally, R/R remained constant as group size changed, regardless of the direction of change. As there are no previous articles identifying these behaviours in relation to group size, it is important to consider what these changes might mean in terms of the functions they serve.

The increase in SDBs as individuals were removed suggests that the chimpanzees became incrementally more uncertain and potentially stressed as group size decreased (and in-group individuals were removed), but uncertainty remained constant as the “super group” was formed. Since SDBs were not significantly correlated with changes in group size as individuals were added, changes in rates of behaviours were not simply a product of the number of individuals present. An additional factor, such as the proportion of in-groups and out-group members, is likely to have played a role (e.g. Wilson et al., 2001 & 2002). Perception of in-group versus out-group interaction is an important factor to consider in the management of animal introductions. How each individual deals with the out-group members determines the eventual outcome of the introductions. If the formation and maintenance of associations and allegiances are important (de Waal, 1982; Goodall, 1986; Newton-Fisher, 1999), as might be expected for a society that is highly fission-fusion dynamic (Aureli et al., 2008), the loss of close allies would be a negative event. Similarly, being reunited with those familiar individuals would be a positive event and might possibly overshadow or balance out the simultaneous addition of unfamiliar individuals, a potentially negative event.

With scratching linked to social changes that can predict negative outcomes (Aureli & de Waal, 1997; Baker & Aureli, 1997) and rubbing potentially linked to changes that do not or are not known to (according to their current knowledge) predict a negative outcome, the increase of both behaviours as individuals were removed would suggest that the chimpanzees were experiencing different types of changes. The decrease in rubbing rates over time (after three months of integration) while other behaviours remained constant, suggests that the chimpanzees were habituating to new circumstances.

In contrast to SDBs, allogrooming was not significantly correlated to group size when individuals were being removed, but did increase as individuals were being added – a logical difference as SDBs are uncertain and potentially stress-related responses (that might have suppressed allogrooming when individuals were removed) while allogrooming is an affiliative behaviour that has been linked to group size (Dunbar, 1991). Or perhaps the increase in allogrooming as individuals were added was in response to the presence of individuals being reunited with familiar individuals and reinforcing existing bonds. Given the nature of in-group/out-group differences, Dunbar's theory on group size (1991) postulated for species difference in group size, might be applied here as there is a mathematical component to associations. Primates spend time grooming to create and maintain relationships and a higher number of individuals could mean a higher number of relationships and subsequent grooming required (Dunbar, 1993; Lehmann et al., 2007), or that more time needs to be spent on current relationships to continue developing alliances. Despite group size doubling with unfamiliar individuals, with a continued interest in in-group grooming, our data suggests the latter; that efforts were made to develop current alliances.

7.5.3 AVAILABLE SPACE IN CAPTIVITY

When considering available space in captivity, the results of this study do not directly translate to previous studies which focused on group density. While group composition frequently changed for the Edinburgh and Beekse Bergen groups as a result of the introduction process, group composition in previous research remained constant (Nieuwenhuijsen & de Waal, 1982; Aureli & de Waal, 1997; Videan & Fritz, 2007). Thinking of the density in terms of low versus high space instead of low versus high density, however, allows a fuller understanding of how enclosure sizes and design relate to behaviour

An analysis of density across the number of available rooms (which extends to the square metre analyses because each size category had a relatively equal distribution of room numbers) ensured that it did not play a role in the results. The available space in terms of the number of rooms and the square metres available varied within the 7.5 months since the introduction process began. Group density decreased from one to two rooms, but remained constant when comparing two to three rooms, which is where we saw a few SDBs decrease, suggesting that those changes were a product of the number of accessible rooms rather than absolute space available or density.

Scratching and yawning decreased as the number of accessible enclosure areas increased from two to three rooms. What is particularly interesting about this finding is that scratching did not decrease as available space increased. This contradicts previous density research where both yawning and scratching increased when less space (high density) was available (Aureli & de Waal, 1997). Since scratching did not decrease as available space increased, it suggests that having the choice of where to be or who to be with may be more important than the amount of space available or total density.

Several researchers have concluded that choice and control is an important part of an animal's life (Badihi, 2006; Meehan & Mench, 2007). By allowing individuals to choose to be together or apart we saw a reduction in SDBs. Zoos are often restricted when it comes to the amount of space available for animal enclosures, but by working with what is available (or when designing new exhibits) and incorporating separate areas or visual barriers into enclosures (e.g. as a part of the naturalised looking indoor exhibit, or through the development of separate "rooms" by strategic plant placement (Simon Jones, personal communication)), the concept of choice can be provided, potentially without the cost of a larger enclosure. This is not to suggest that the amount of space is irrelevant. While space should always be a consideration for the species being housed for physical exercise and other reasons, the number of separate areas within the enclosure also seems to be of great importance for the psychological health of the animal.

With regards to R/R, however, no changes were seen in relation to the number of rooms or available space. It is important to remember that nearly everything in the lives of the Beekse Bergen group had recently changed and they were continually getting used to the new environment, new staff, and new chimpanzees. Even though other behaviours were influenced by enclosure availability, this might suggest that for this group of chimpanzees, space restrictions (Lukas, 1999) were not the underlying reason behind their performance of R/R.

The variety of enclosure areas (the pods) within Budongo Trail exhibit offers the residents many choices. The Beekse Bergen group showed a preference for the smaller, off-exhibit area (mostly with in-group individuals). Having the freedom to choose to be in this preferred area might have assisted in their adjustment to life in this new enclosure and in the "super group". The challenging side to the beneficial

nature of choice is striking a balance between what is best for the animal: tending to the animals' need for physical exercise and to benefit from being outdoors in nice weather (e.g. vitamin D from the sun) with their need to "feel safe" indoors in smaller areas. This topic is likely to be an on-going challenge for zoos, particularly as animals whom have had atypical backgrounds (e.g. laboratory chimpanzees like the Beekse Bergen group, for more on their background, see Chapter 2) become a part of their collection in the endeavour to create "natural" group compositions and for chimpanzees, to increase the *Pan troglodytes verus* population.

The pattern of allogrooming reported here also contradicts previous evidence, where it decreased as the available space (number of rooms) increased (Aureli & de Waal, 1997; Videan & Fritz, 2007). Considering the density analysis, since this difference was limited to the change from one room to two rooms, it was likely due to a decrease in density as opposed to the number of rooms. Although we do not have detailed data on aggressive behaviours throughout the enclosure during the introduction process, the increase in allogrooming during the periods of high density could suggest the chimpanzees employed grooming to reduce tension (de Waal, 1989) by increasing affiliative behaviours in the short term. Even though the space and social changes were temporary, the higher frequency of changes associated with introductions seemed to be viewed by the chimpanzees as a long-term conflict situation. Perhaps this suggests that the distinction between the short- and long-term conflict management models does not fit the unique situation of chimpanzee introductions where experiences are perceived with greater intensity.

7.5.4 GROUP TRANSFER OF ABNORMAL BEHAVIOUR

R/R has been suggested be able to transfer across individuals through social learning (Hook et al., 2002). The reason for this is unknown, and as Hook et al. (2002) suggested, additional studies exploring the learning process behind group transfer of abnormal behaviour are needed. Fortunately for the Edinburgh group, who had no known experience with R/R, the behaviour did not transfer across groups. This lack of group transfer does not help clarify the reasoning behind social learning of abnormal behaviour, but does provide evidence that it is not an inevitable occurrence. Introducing groups with individuals who engage in R/R does not necessarily indicate that the behaviour will spread and should

not be a deterrent from introducing individuals which otherwise would be ideal matches from both a genetic and behavioural standpoint. In addition to social learning, research efforts should continue to focus on the underlying causes of the abnormal behaviour (e.g. Baker & Easley, 1996; Lukas, 1999; Struck et al., 2007).

7.5.5 INTERGROUP ASSOCIATIONS

The social mixing between the Edinburgh and Beekse Bergen groups was the entire reason behind the introduction process. One year after the introductions began the chimpanzees have yet to determine their new hierarchy. While being integrated as one group may only mean living in the same area instead as living as one social group it is hoped that social mixing will increase over time allowing individuals to develop relationships and build alliances.

The chimpanzees chose to be within the same enclosure space as out-group chimpanzees (i.e. at least one individual from Edinburgh with Beekse Bergen and vice versa) during 48.7% of the Integration phase. In that time when they had the choice to mix, they participated in allogrooming approximately 5% of the time. In accordance with the hypothesis, the estimated percentage of time spent allogrooming was highest with in-group chimpanzees. Contrary to the hypothesis, there was no difference in grooming out-group chimpanzees between groups or sexes. The individuals from the Beekse Bergen group were expected to groom out-group chimpanzees (individuals from the Edinburgh group) more than the Edinburgh group given that they were less established (introduced to each other in 2007) compared to the Edinburgh group (same composition since 1999 and many longstanding group members). Since the results remained constant throughout the Integration phase (the first three weeks and the last three weeks), it is clear that substantial intergroup relations have not developed. While 7.5 months is a short duration to study the development of group formation, it is encouraging to see grooming of out-group individuals at all. Only time will tell how the group structure will progress.

7.5.6 ALLOGROOMING: RELATIONSHIPS BETWEEN SEX, KIN, AND RANK

Social relationships with males were expected to be more important to males than females given the strategic and political nature of chimpanzee associations (de Waal, 1982; Goodall, 1986; Newton-Fisher, 1999). Males are generally more dominant than female chimpanzees, so it would make sense to build

relationships with males through allogrooming to gain their support. The lack of a sex difference in rates of grooming males suggests that both sexes value the support of males equally. This extends to in-group and out-group males; while in-group individuals are groomed more often than out-group individuals, neither sex is capitalising upon the opportunity to use grooming to win over the males within the “opposing” group, although some individuals may be using this strategy (see outliers).

Although kin are reported to engage in more allogrooming than non-kin (de Waal, 1978), we found no effect of kin on overall grooming. Individuals without kin in the group participate in grooming (and subsequently building/maintaining relationships) just as much as those with kin in the group. There was also no difference between those who were aware of their kin status and those who had kin, but may not know it (not raised together or identified by DNA tests). The importance of the kin relationship was only revealed during the Integration phase when the grooming of kin significantly increased following the merge of the two groups.

Rank of the recipient had no bearing on allogrooming by either sex, but it was positively correlated with percentage of time spent allogrooming. In other words, higher ranked individuals engaged in more grooming, but rank did not impact upon the likelihood of receiving grooming. This supports the concept that more dominant individuals would need the support of those around him/her in order to be higher ranking (de Waal, 1982).

7.6 SUMMARY AND CONCLUSIONS

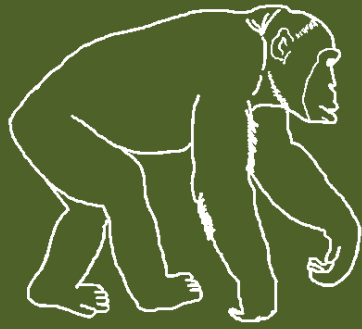
The goal of the chimpanzee introductions was to create a larger, more natural group (in size and composition), where individuals were socially enriched and in following guidance from the studbook keeper, were allowed to breed (Visalberghi & Anderson, 1993). Overall the data suggest that the introduction process did not compromise welfare to a significant degree. The Mix phase, when individuals were being removed from their original groups to become a part of the “super group”, had high levels of rubbing which decreased as soon as the two groups were merged into one. The speed and care with which the animal management team took to carry out the introductions ensured that the Mix phase, while necessary, occurred as swiftly as possible.

A detailed look into the Mix phase showed that individuals performed higher rates of rubbing and R/R in the condition when individuals were removed compared to when they were added. Group size also played a large role during this phase as all SDBs increased in the time period between each individual (or pair) were removed from their original groups and remained constant over time (with the exception of rub, which decreased). The differing use of rub compared to scratch during potentially stressful situations prompted the idea that the function of rubbing might be linked to uncertain or potentially stressful and frustrating changes that do not (or are not known to) have the potential to produce negative outcomes.

Allogrooming occurred an average of 5% of each chimpanzee's day. This grooming behaviour changed in response to group size and was performed on in-group individuals far more than out-group individuals (though a small percentage of out-group grooming did take place) reinforcing the concept that it plays a role in building strategic alliances. Grooming did not appear to differ across males and females. While rank of the recipient had no bearing on the percentage of grooming by either sex, rank was positively correlated with grooming.

Even though the analyses contradict a few of the suggested functions of R/R, it would not be appropriate to suggest that those reasons (i.e. space restrictions, stress, and lack of control) be removed from the list of potential functions. Only being able to analyse data on one of the two groups of chimpanzees, the sample size was small. It is also important to emphasise actual stress in animals' might be different than how we, as humans, perceive it; therefore it would be helpful to continue research addressing the underlying causes of R/R.

The new group of 22 chimpanzees at Budongo Trail experienced many changes over the last 7.5 months. Anecdotally speaking, once the group was fully formed, more time seemed to be spent on inter-group aggression, because even though the groups had merged, they were still living as separate groups defending their territory. Challenges will continue to arise in the future, but now that the introductions are complete, the challenges ahead will be familiar ones (dominance struggles, etc.), just within a larger group.



CHAPTER 8

CONCLUSIONS



CONCLUSIONS

8.1 SUMMARY

This research project critically evaluated the development of a cognitive research programme and chimpanzee introductions in a zoo. Throughout this project, we have learnt that chimpanzees are resilient to change, be it social or cognitive; research naïve individuals need time and attention to understand cognitive tasks; their personalities and behaviours in response to video footage of unfamiliar individuals can predict how they will behave when they physically meet these individuals. In addition, the public is willing to engage in science through popular forms of media where intended messages are likely to be received and incorporated into viewer opinion. However, this may reflect ceiling effects, with the individuals sampled already demonstrating engagement with science-related activities. Additional discussion of the research strands within this study, recommendations, and directions of future research are summarised in the following sections.

8.1.1 DEVELOPMENT OF A COGNITIVE RESEARCH PROGRAMME

For the chimpanzees of Budongo Trail, cognitive research was a new challenge. As this project was the facility's first research endeavour, it was important to establish the chimpanzees' interest and performance in research activities as a baseline for future projects. The exhibit, combined with the numerous activities the keepers provided, represented one of the biggest competitors that the research had for the chimpanzees' attention. This group was not at a loss for things to do; research sessions were just another choice they had in the day. Despite some individual variation, their repeated participation in the research suggests that, overall, they found the activities to be enriching and mentally stimulating. However their performance in the touchscreen task suggests that more intensive training over a longer period of time was needed to help understand the activity (e.g. Biro & Matsuzawa, 2001), or that the stimuli provided in the video feeds was not of interest to the chimpanzees.

While methodological details might impact upon on engagement and uncertainty in training and testing sessions, for example task difficulty (Leavens et al., 2001), or visual access to keepers, no factor sufficiently increased SDBs to levels which might indicate that these activities were impacting negatively upon wellbeing. Despite a lack of formal consensus regarding species-typical rates of SDBs, as there is a

lot of variation between and within chimpanzee groups (e.g. Baker & Aureli, 1997; Leavens et al., 2004; Kutsukake, 2003a; Hockings, 2007), assessments of the impact changes in SDBs have on welfare are able to be made on an individual or group basis with care staff. A closer look at two methodological variations within the Research Pod Activities revealed that while contingency of rewards did not impact SDB rates, having visual access to keepers during training and testing did; a potential by-product of previous training experiences. Social context, rank, or participation did not seem to impact upon SDB or vigilance rates (unlike data on rank and SDBs from Kutsukake, 2003a, and anecdotal evidence on vigilance from Leighty et al., 2011), suggesting that the potential variables impacting the measures of welfare were equal, leaving the differences to be from individual variation (e.g. Yamanashi & Matsuzawa, 2010).

The public's perception of the research conducted in zoos might not always match our preconceived intentions, so assessing opinions from our audiences can help to assess the impact of our public engagement activities. Studying PES also helps us gain a better understanding of how our supporters view our work and if any areas need attention, we can address them in the continued hope that by creating an environment of understanding, we might better conserve the species we study (e.g. Ballantyne & Packer, 2005; Falk et al., 2007). By producing a documentary about the trials and tribulations of conducting cognitive research with a group of research naïve chimpanzees, we were able to reach international audiences with a research project that otherwise would most likely have had a limited reach within the academic and zoo communities.

Although systematic assessment of the impact of nature documentaries on viewer opinion is rare, the documentary, the Chimpcam Project, followed suit with previous findings (Barbas et al., 2009). It had a positive influence on public opinion in areas of concern to the research within the film, particularly how they view zoo research, scientists, overall welfare in zoos, and the importance of choice for animals. In choosing a documentary as our primary method of public engagement with secondary methods that provided different learning opportunities (e.g. passive entertainment through the YouTube clip and more in-depth knowledge through the project website, www.chimpcam.com), we tapped into audiences' interest by using popular media; a medium with which most people are likely to interact.

8.1.2 CHIMPANZEE INTRODUCTIONS

After completion of the research tasks, the group continued to face species-typical challenges in their everyday lives much like those described by Goodall (1971) for wild and de Waal (1982) for captive chimpanzees. When the chimpanzee introductions began, these challenges changed in form and frequency; new individuals were being introduced and the management process to safely merge the two groups was something that neither of these groups had experienced on this level before (i.e. group of 11 meeting a group of 11). The cognitive thread within the project was carried into this strand of research with the use of video footage to observe the unfamiliar individuals they were about to meet.

While the Edinburgh group's interest in the live-video feeds from around their enclosure (Chapter 3) was limited, a few of the individuals expressed repeated interest in the video introduction footage (Chapter 6), however, this paled in comparison to the interest from the Beekse Bergen group as the majority of the time, all 11 individuals opted to be in the two bed areas available when video introductions were shown. Perhaps cognitive activities with video footage may only be useful for those who are interested in watching at all. Based on this information, if the cognitive testing could be developed with the Beekse Bergen group, the training outcomes and research results might be very different. While it is clear that individual differences play a role in participation and interest in activities, group differences might also reflect early life histories in terms of physical and social stimulation received (Furlong et al., 2008). Although enculturated chimpanzees have been shown to perform better on tool-use tasks than semi- or non-enculturated chimpanzees (Furlong et al., 2008), differences between zoo-raised and laboratory-raised chimpanzees have not been tested (Hosey, 2005), particularly for those who have not regularly participated in cognitive tasks.

Despite the new challenges encountered during the introduction process, changes in SDBs were minimal, much like those during the development of the cognitive research programme. From an outsider's perspective, we would certainly say that the challenges faced during the introductions were much more stressful than those faced during the cognitive research activities. However, despite these differences, the chimpanzees' reactions in terms of SDBs show how resilient they are to change as well as cognitive and social challenges (e.g. Byrne & Whiten, 1988; Stokes & Byrne, 2001; Hockings et al.,

2006). Additionally, despite recent concerns about the prevalence of R/R behaviour within captive chimpanzees (Birkett & Newton-Fisher, 2011), given that R/R did not transfer across groups, concerns about group transfer of abnormal behaviours should not heavily influence management decisions when considering the composition of adult groups. However, it is important to note that additional factors surrounding the group (e.g. living in a facility designed to relieve some of the stressors of captivity that are suggested to serve as an underlying behaviour of R/R; as reviewed by Lukas, 1999) most likely played a role in why the behaviour seemed to be reduced in the incoming group and also did not transfer to the resident group.

Introducing unfamiliar chimpanzees to each other represents a very intense social challenge. Several animal management techniques were used during the introduction process to encourage interaction between groups and minimise risk for both chimpanzees and keeping staff. By assessing the predictive power of different measures within the introduction process we could minimise risk even further. The absence of a predictive relationship between the behaviours seen during the visual access period and behaviours during the physical introductions suggests that while possibly helpful as an outlet for initial aggression, the social behaviours seen during this time did not help anticipate how individuals will react in one-on-one or small group introductions. This is particularly important as visual access periods are common practice during the introduction process (e.g. Fritz & Fritz, 1979; Noon, 1991; McDonald, 1994; Alford et al., 1995; Brent et al., 1997; Seres et al., 2001; Fritz & Howell, 2001).

Personality factors (Weiss et al., 2009) and video introductions, on the other hand, had predictive power; certain personality factors (i.e. subjective ratings from the keepers and researcher) were the clearest indicators of how different individuals were likely to behave during introductions. On a theoretical level, this is an important contribution to our understanding of personality measurement in other species; while personality should help to predict behaviour, there is seldom a means of assessing this beyond the context in which observations and ratings were themselves made. Moreover, since assessing personality is a low-cost measure that can provide information on the chimpanzees that are even unfamiliar to the keepers managing the introductions (when completed by their original keepers),

it appears to be the most effective method to assist animal management within the introduction process.

8.2 RECOMMENDATIONS

In studying the unusual events of developing a cognitive research programme with research naïve chimpanzees and the introduction of unfamiliar individuals, the following recommendations have been outlined as take-home messages for zoo professionals:

8.2.1 WELFARE

- (1) SDBs should be reported independently rather than lumped together in general categories. When SDB data follow the same patterns and are reported together, supplementary data noting specifics should be provided as systematic comparisons are difficult with combined data.
- (2) SDBs are useful measures of uncertainty (Maestriperi et al., 1992). Scratching has been linked to social change that predicts negative outcomes (Baker & Aureli, 1997), but the function behind other SDBs, such as rubbing and yawning, has not yet been identified. Based on the studies within this thesis, the SDB of rubbing might best be viewed as having a different motivational drive than scratching during potentially stressful situations, indicating that the situation is viewed as uncertain (in that they do not know how to behave), but not necessarily a negatively valenced context that is predictive of a socially negative outcome.
- (3) Enclosure space matters to chimpanzees (Ross et al., 2009), but the number of rooms is more important than the total amount of space. When designing or refitting enclosures, multiple rooms or visual barriers should be provided to allow the chimpanzees to exercise choice (Markowitz, 1982 as cited in Badihi, 2006) over where they are and with whom they are near. This may slightly decrease visibility to visitors, but in addition to the welfare benefit, it could be used as an opportunity to inform visitors about the psychological needs of animals and allow them to engage in some of the behaviours needed to observe chimpanzees in the wild (i.e. keen observation skills and a bit of patience).

8.2.2 RESEARCH MANAGEMENT

- (1) Training and testing for cognitive research can be conducted without isolating individuals (i.e. in a group context) provided that additional trainers are available to distract the majority of the chimpanzees or increased access to the research apparatus is provided (if automated, e.g. Fagot & Paleressompulle, 2009) in order to provide all individuals with the opportunity to participate.

8.2.3 PUBLIC ENGAGEMENT WITH SCIENCE

- (1) Media (i.e. film, websites, etc) can be effective tools in engaging the public with science. Research endeavors should be presented to the public in an easily digestible format (in which they are likely to engage) to increase awareness and positively influence opinions of zoo research as a whole.
- (2) A lot of time and money has been invested into PES endeavors, but the evaluation of its impact is not always measured. Both reach and depth of the PES should be examined to inform best practices. Although attendance to an event has been used as a fairly easy way to assess impact, it should not be the sole measure used. Additional assessments of participant opinions and secondary forms of PES (e.g. visitor numbers to project websites) can measure perceived value and show interest over time (i.e. participation after the original event shows further interest and follow-up on behalf of the initial audience). Further research should be conducted to develop methods to examine both short- and long-term behavioural changes in relation to PES.
- (3) Since the chimpanzees reacted similarly to training/research activities that were both off- and on-public display, more opportunities should be taken to allow the public to see what researchers do first hand. The result of viewing a documentary about the research held in Budongo Trail increased awareness about zoo research and influenced the viewers' understanding of what we do to learn more about the animals in our care.

8.2.4 CHIMPANZEE INTRODUCTIONS

- (1) When faced with the daunting task of introducing unfamiliar chimpanzees to each other, personality profiles can be used as a low-cost method of identifying factors to predict behaviours during physical introductions. The continued use of this method can assist in animal management

decisions as well as support the utility and validity of personality research in non-human primates (e.g. Dutton et al., 1997; King & Figueredo, 1997; Uher et al., 2008; Weiss et al., 2009; Freeman et al., 2011).

- (2) Even though behaviours seen during the visual access period did not predict behaviours during the physical introductions (similar to previous research; Brent et al., 1997), changes in behaviour over the course of the introductions, namely an increase in passive behaviours from the visual access period (Bloomsmith et al., 1998) suggest that a visual access period would be helpful to provide an outlet for initial aggression (false bravado) when working with large group introductions.

8.3 FUTURE DIRECTIONS

When assessing the needs of an animal in response to learning and social challenges, individual variation inevitably plays a role. Despite the challenges of conducting cognitive and behavioural research in a zoo, the positives outweigh the negatives. Not only are we able to learn about our closest living relative through research, but we are able to enhance their welfare, and serve as a voice for conservation. Chimpanzees are amazing creatures and despite being regularly studied in captivity (e.g. Yerkes, 1939; Menzel, 1973; Matsuzawa, 1985; Itakura, 1993; Parr, 2001; Ross et al., 2009; Yamanashi & Hayashi, 2011) and in the wild (e.g. Goodall, 1971; Nishida, 1979; McGrew, 1979; Boesch & Boesch, 1984; Newton-Fisher, 1999; Whiten et al., 1999; Morgan & Sanz, 2003; Nakamura, 2003; Muller & Wrangham, 2004; Lonsdorf, 2005), they have a great deal more to teach us about their world.

8.3.1 COGNITIVE RESEARCH

With the addition of the cognitive research programme, the chimpanzees were eager to interact with the touchscreen, future research would benefit from following up on the technological addition to their cognitive arsenal and focus training efforts on a task with a clear answer (as opposed to a free-choice activity). In their experiences thus far (outside of the video choices study), their training activities have had prompts with behavioural responses required to earn a reward. Perhaps they would perform more reliably with activities that were clear cut and followed a familiar pattern (prompt/behaviour/reward);

Alternatively, research efforts involving video could focus on individuals who are already interested in watching video footage (i.e. the Beekse Bergen group instead of the Edinburgh group).

8.3.2 BEHAVIOURAL ASSESSMENTS OF WELFARE

Behavioural assessments of welfare can be enhanced with the use of non-invasive physiological measures (e.g. cortisol); however, the interpretation of these measures can be challenging (i.e. responses to good versus bad stress, de Kloet et al., 1999). The ability of behavioural measures to assess the immediate impact of an event on an individual allows for easier assessment of responses to short-term events, such as those within cognitive testing; however, the addition of non-invasive physiological measures could be useful during longer-term social stressors (i.e. chimpanzee introductions) to provide a new look into the physiological reactions of chimpanzees meeting unfamiliar individuals (e.g. cortisol or oxytocin; reviewed by Taylor et al., 2000) as well as validate current behavioural measures.

8.3.3 SOCIAL DYNAMICS

As the newly formed group develops, efforts to maintain or develop new coalitions will inevitably impact their social network (Clark, 2011) and possible transfer of knowledge (Buchanan, 2011). Their in-/out-group dynamics (e.g. Sherif et al., 1961; Campbell & de Waal, 2011; Mahajan et al., 2011) can teach us not only about the social aspect of the chimpanzee mind (e.g. in relation to human social psychology and its evolutionary origins), but to also aid management practices. Differences in these dynamics suggest that chimpanzees have a social identity not only as individuals, but as cohesive groups. Will it only be a matter of affiliative interactions that are needed for these two groups to become one? Or, are additional factors involved (e.g. uniting over a common enemy, overcoming competitors through physical interactions, or outsmarting each other within their Machiavellian world)?

Carefully managed introductions are required to safely merge the two groups, at which point group structure and cohesion are dependent upon the members of the group. With measures such as personality profiles and behaviours during video introductions shown to predict how chimpanzees behave when facing unfamiliar individuals, there is great potential for these measures to assist animal management teams. These measures are not only helpful as introductions are happening (e.g. helping

keepers become familiar with the new chimpanzees), but with more research, could potentially benefit the early planning stages of animal transfers.

Captive social groups are often selected based on genetics when breeding is a possibility. Additional qualitative consideration is given to the individuals' life histories and social interactions in terms of whether or not they will integrate well with others. While qualitative descriptions are valuable to the understanding of each individual, an established quantitative measure, such as personality profiles (Weiss et al., 2009), could be incorporated into studbook records for easy access of information. Additional research focusing on the role of personality and video introductions in successful and unsuccessful group combinations can potentially avoid the stress of animal transfers and introductions for what could likely be incompatible groups.

8.3.4 ATYPICAL EARLY LIFE HISTORIES

Within this project, we were able to study both zoo- and laboratory-raised chimpanzees. While outside of the scope of this thesis, during our studies, differences between the zoo and laboratory groups appeared (e.g. the laboratory group appeared to have a preference to be closed into small, off-exhibit areas and not venture outside, exhibited R/R and other abnormal behaviours, etc.). As various countries have stopped biomedical research with chimpanzees (and the United States working on legislation now; e.g. Project ChimpCARE), animal care staff are now faced with the challenge of caring for chimpanzees, this is especially challenging as individuals have extremely different life histories and potentially vary in relation to important emotional and social behaviours, as well as in their capacity to cope with challenges. Additional research examining these atypical life histories can benefit the fields of welfare (e.g. long-term care for former biomedical chimpanzees, for example, resilience in adulthood following restricted early life experiences), animal management (e.g. can too much choice be bad for individuals who have species-atypical preferences?), social psychology (e.g. how does life experience impact one's ability to maintain social relationships in accordance with their group's norms?), and abnormal psychology (e.g. the evolutionary history of human abnormal behaviour).

8.3.5 FINAL THOUGHT

This thesis assessed the development of a cognitive research programme and chimpanzee introductions in a zoo. In order to provide the best welfare for the chimpanzees in our care, we need to understand how research and management practices affect their lives and how the public interpret what we do as researchers. By understanding these aspects of their world and accepting our responsibility to serve as a voice for animals, we can better serve those in captivity, influence public opinion on the importance of conserving those in the wild, and ultimately help us understand the evolutionary origins of humans.

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APPENDIX A: DOMINANCE RANKINGS

APPENDIX A1: EDINBURGH GROUP DOMINANCE RANKINGS

Chimpanzee	Rank	Average rating	Researcher	Keeper 1	Keeper 2	Keeper 3
Cindy	11	10.75	11	10	11	11
David	2	2.5	2	2	4	2
Emma	4	3.5	4	4	2	4
Kilimi	8	8.25	9	8	8	8
Kindia	5	5.25	5	5	6	5
Liberius	7	8	7	9	9	7
Louis	3	3	3	3	3	3
Lucy	6	5.75	6	6	5	6
Lyndsey	9	8.5	8	7	10	9
Qafzeh	1	1	1	1	1	1
Ricky	10	9.5	10	11	7	10

Note: Individuals of the Edinburgh group were ranked according to dominance by the researcher and three keepers based on their observations of all known behaviours, most notably aggression, submission, priority access to areas, and support received during fights (January 2009). Average ratings were calculated across observers and then ranked on a scale from 1 – 11 with one being the highest ranking and 11 being the lowest ranking. The rankings were split into categories of high, medium, and low (as shown in Figure 3.1), where ranks 1 – 4 were high, 5 – 7 were medium, and 8 – 11 were low. For information on inter-observer reliability, see chapter 2.

APPENDIX A2: BEEKSE BERGEN GROUP DOMINANCE RANKINGS

Chimpanzee	RANK	Average score	Personality trait score: Dominance (Keeper 1)	Personality trait score: Dominance (Keeper 2)
Bram	6	4	6	2
Claus	1	6.5	7	6
Edith	8	3	4	2
Eva	3	6	6	6
Frek	7	3.5	3	4
Heleen	9	2.5	4	1
Lianne	11	1	1	1
Paul	2	6	6	6
Pearl	4	5.5	6	5
Rene	5	5	5	5
Sophie	10	1.5	2	1

Note: Individuals of the Beekse Bergen group were ranked according to information received from two of their keepers (2010). Both keepers completed a personality survey (Weiss et al., 2009) where they were asked to rate each chimpanzee on a number of behaviours, including dominance (see Chapter 5). In the survey, dominance was defined as, “Subject is able to displace, threaten, or take food from other chimpanzees. Or subject may express high status by decisively intervening in social interactions.” With a rating scale from 1 (absence of trait) to 7 (large amounts of trait), rankings were calculated by averaging the two scores for each chimpanzee and listing the highest rank for the highest average score through the lowest rank for the lowest score. When an average score was the same for two individuals (a male and a female), the higher rank went to the male. The rankings were split into categories of high, medium, and low (as shown in Table 2.2), where ranks 1 – 4 were high, 5 – 7 were medium, and 8 – 11 were low. For information on inter-observer reliability and how this compares to the Edinburgh group dominance rankings, see Chapter 2.

APPENDIX B2: CHAPTER 4 – BEHAVIOURS (VIDEO CODING)

Chimp:

Condition:

Observer:

Total:

Total clips:

OOS:

(s)

Date coded:

Video file	Video segment				Scratch		Rub	Yawn	Self groom	Other	Stand	Look	Rewards		
	Start	End	OOS	(s)	Fingers only	All others							Earned	Stolen	Found
TOTAL - alone (marks are NOT blue)															
TOTAL - with others (marks are in blue)															
GRAND TOTAL															

APPENDIX B3. CHAPTER 4 – INTEREST IN RESEARCH (SEE SECTION 4.2.4)

One-minute scan samples of location within Research Pods													Date:						Start time:						End time:						Legend: X = in pods X. = in tunnel T = at test window
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
Cindy																															
David																															
Emma																															
Kilimi																															
Kindia																															
Liberius																															
Louis																															
Lucy																															
Lyndsey																															
Qafzeh																															
Ricky																															

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	Notes:
Cindy																															
David																															
Emma																															
Kilimi																															
Kindia																															
Liberius																															
Louis																															
Lucy																															
Lyndsey																															
Qafzeh																															
Ricky																															

APPENDIX B4. CHAPTER 5 – SURVEY

The Chimpcam Project: Public Perception Survey

This survey will only take 5-10 minutes to complete.

Name of survey guide: _____

Date: _____

Time: _____

Please check one box per category/question:

Group composition: Alone Group of adults Group with children

(1) Gender: Male Female

(2) Age: 12 & under 13-19 20-29 30-39 40-49 50-59 60 +

(3) Which country do you live in?

Scotland England Wales N. Ireland USA Other _____

(4) On average, over the past five years, how often have you visited zoos, aquariums, or science centres each year? 0 1 2 3 +

(5) How many times have you visited the chimpanzee exhibit, Budongo Trail at Edinburgh Zoo? 0 1 2 3 +

(6) Compared to last year, this year do you think you will visit zoos, aquariums, or science centres:

More Less Same

(7) How would you rate your knowledge of animals and nature?

Expert General Limited Not interested

(8) How would you rate your knowledge of chimpanzees?

Expert General Limited Not interested

(9) How often do you watch nature documentaries each year?

Never On occasion Monthly Weekly or more

For the following statements, please select the option that you agree with most:

(10) People can learn a lot about animals from watching wildlife programmes. 1 2 3 4 5

(11) I am more likely to support conservation and welfare campaigns after watching wildlife programmes. 1 2 3 4 5

(12) Did you watch the recent documentary on the chimpanzees at Edinburgh Zoo "The Chimpcam Project"? Yes No

IF NO: PROCEED TO #16

IF YES: Select the option that you agree with most:

(13) I learned a lot about chimpanzee cognition from watching the documentary "The Chimpcam Project" 1 2 3 4 5

(14) I learned more about the type of research that can be carried out within the zoo 1 2 3 4 5

(15) I do not think that chimpanzees enjoy being challenged with new research tasks. 1 2 3 4 5

The research in Budongo Trail allows the chimpanzees the choice to participate or not, and does NOT cause them any discomfort. Dedicated research areas are in full public view.

(16) I think it is a good idea for zoos to host this type of research (as defined above) with chimpanzees. 1 2 3 4 5

(17) I am not interested in watching the scientists at work within the zoo. 1 2 3 4 5

(18) I would like to be able to talk to scientists working in the zoo. 1 2 3 4 5

(19) Research (as defined above) with animals is a career that I would consider for my future. 1 2 3 4 5

(20) I am less likely to visit a zoo that is involved in research (as defined above). 1 2 3 4 5

(21) Animals should not have a choice when it comes to participating in research (as defined above). 1 2 3 4 5

(22) The Budongo Trail chimpanzees lead a better life compared to chimpanzees in other UK zoos. 1 2 3 4 5

(23) Zoo chimpanzees are more intelligent than wild chimpanzees. 1 2 3 4 5

(24) I do not think chimpanzees experience emotions. 1 2 3 4 5

(25) Animal welfare in zoos has not changed in the past 20 years. 1 2 3 4 5

(26) To ensure the survival of wild chimpanzees, conservation programmes are vital. 1 2 3 4 5

(27) Have you visited the chimpcam.com website? Yes No

Comments:

APPENDIX B6. CHAPTER 6 – PHYSICAL INTRODUCTIONS

Introduction evaluations

- Based on your subjective opinion, provide a % the behavioural categories for each chimp (should total 100%)
- Rate the chimps in the EVALUATE column against 'Overall' for the duration of the intro and 'Individuals they met'
- If you cannot accurately assess a pairing, please omit. Behavioural definitions can be found in this folder

Date:

Length/Duration:

Evaluator:

EVALUATE	Overall	INDIVIDUALS THEY MET:								Behavioural categories
█		█								AGG
										AFF
										SUB
										Neutral
										Not there
□			█							AGG
										AFF
										SUB
										Neutral
										Not there
█				█						AGG
										AFF
										SUB
										Neutral
										Not there
□					█					AGG
										AFF
										SUB
										Neutral
										Not there
█						█				AGG
										AFF
										SUB
										Neutral
										Not there
□							█			AGG
										AFF
										SUB
										Neutral
										Not there
█								█		AGG
										AFF
										SUB
										Neutral
										Not there

APPENDIX B7. CHAPTER 6 – VIDEO INTRODUCTIONS

First two pages of the checksheets for the Edinburgh Group (Qafzeh’s) during video introductions. The second two pages follow the same pattern and show the second 30 minutes of the session. Checksheets for the Beekse Bergen group follow the same format with names changed appropriately. The black spaces above each five-minute block of time allow the observer to note which video was watched.

Group:	QAFZEH	Condition:	Date:	Start time:																											
Legend: A = Look away = Watch	W T = In Tunnel O = In adjacent bed	W in circle = watching from adjacent bed	Observation area = Bed nearest the monitor	Note: Data covers group presence in the monitor area																											
	0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8	8.5	9	9.5	10	10.5	11	11.5	12	12.5	13	13.5	14	14.5	15	
Cindy																															
David																															
Emma																															
Kilimi																															
Kindia																															
Lib																															
Louis																															
Lucy																															
Lynds																															
Qafzeh																															
Ricky																															

	15.5	16	16.5	17	17.5	18	18.5	19	19.5	20	20.5	21	21.5	22	22.5	23	23.5	24	24.5	25	25.5	26	26.5	27	27.5	28	28.5	29	29.5	30	
Cindy																															
David																															
Emma																															
Kilimi																															
Kindia																															
Lib																															
Louis																															
Lucy																															
Lynds																															
Qafzeh																															
Ricky																															

APPENDIX B8. CHAPTER 6 – PERSONALITY QUESTIONNAIRE**CHIMPANZEE PERSONALITY TRAIT ASSESSMENT**

Chimpanzee personality assessments can be made with this questionnaire by assigning a numerical score for all of the personality traits listed on the following pages. Make your judgments on the basis of your own understanding of the trait guided by the short clarifying definition following each trait. The chimpanzee's own behaviors and interactions with other chimpanzees should be the basis for your numerical ratings. Use your own subjective judgment of typical chimpanzee behavior to decide if the chimpanzee you are scoring is above, below, or average for a trait. The following seven point scale should be used to make your ratings.

1. Displays either total absence or negligible amounts of the trait.
2. Displays small amounts of the trait on infrequent occasions.
3. Displays somewhat less than average amounts of the trait.
4. Displays about average amounts of the trait.
5. Displays somewhat greater than average amounts of the trait.
6. Displays considerable amounts of the trait on frequent occasions.
7. Displays extremely large amounts of the trait.

Please give a rating for each trait even if your judgment seems to be based on a purely subjective impression of the chimpanzee and you are somewhat unsure about it. Indicate your rating by placing a cross in the box underneath the chosen number.

Finally, do not discuss your rating of any particular chimpanzee with anyone else. As explained in the handout accompanying this questionnaire, this restriction is necessary in order to obtain valid reliability coefficients for the traits.

CHIMPANZEE PERSONALITY TRAIT ASSESSMENT

Chimpanzee's full name: _____

Rater's full name: _____

Date (Mon/Day/Yr): _____

FEARFUL: Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.

least most

1 2 3 4 5 6 7

DOMINANT: Subject is able to displace, threaten, or take food from other chimpanzees. Or subject may express high status by decisively intervening in social interactions.

least most

1 2 3 4 5 6 7

PERSISTENT: Subject tends to continue in a course of action, task, or strategy for a long time or continues despite opposition from other chimpanzees.

least most

1 2 3 4 5 6 7

CAUTIOUS: Subject often seems attentive to possible harm or danger from its actions. Subject avoids risky behaviors.

least most

1 2 3 4 5 6 7

2

STABLE: Subject reacts to its environment including the behavior of other chimpanzees in a calm, equable, way. Subject is not easily upset by the behaviors of other chimpanzees.

least most

1 2 3 4 5 6 7

AUTISTIC: Subject often displays repeated, continuous, and stereotyped behaviors such as rocking or self claspng.

least most

1 2 3 4 5 6 7

CURIOS: Subject has a desire to see or know about objects, devices, or other chimpanzees. This includes a desire to know about the affairs of other chimpanzees that do not directly concern the subject.

least most

1 2 3 4 5 6 7

THOUGHTLESS: Subject often behaves in a way that seems imprudent or forgetful.

least most

1 2 3 4 5 6 7

3

STINGY/GREEDY: Subject is excessively desirous or covetous of food, favored locations, or other resources in the enclosure. Subject is unwilling to share these resources with others.

least most

1 2 3 4 5 6 7

JEALOUS: Subject is often troubled by others who are in a desirable or advantageous situation such as having food, a choice location, or access to social groups. Subject may attempt to disrupt activities of advantaged chimpanzees.

least most

1 2 3 4 5 6 7

INDIVIDUALISTIC: Subject's behavior stands out compared to that of the other individuals in the group. This does not mean that it does not fit or is incompatible with the group.

least most

1 2 3 4 5 6 7

RECKLESS: Subject is rash or unconcerned about the consequences of its behaviors.

least most

1 2 3 4 5 6 7

4

SOCIABLE: Subject seeks and enjoys the company of other chimpanzees and engages in amicable, affable, interactions with them.

least 1 2 3 4 5 6 7 most

DISTRACTIBLE: Subject is easily distracted and has a short attention span.

least 1 2 3 4 5 6 7 most

TIMID: Subject lacks self confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.

least 1 2 3 4 5 6 7 most

SYMPATHETIC: Subject seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance.

least 1 2 3 4 5 6 7 most

PLAYFUL: Subject is eager to engage in lively, vigorous, sportive, or aerobic behaviors with or without other chimpanzees.

least 1 2 3 4 5 6 7 most

5

SOLITARY: Subject prefers to spend considerable time alone not seeking or avoiding contact with other chimpanzees.

least 1 2 3 4 5 6 7 most

VULNERABLE: Subject is prone to be physically or emotionally hurt as a result of dominance displays, highly assertive behavior, aggression, or attack by another chimpanzee.

least 1 2 3 4 5 6 7 most

INNOVATIVE: Subject engages in new or different behaviors that may involve the use of objects or materials or ways of interacting with others.

least 1 2 3 4 5 6 7 most

ACTIVE: Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.

least 1 2 3 4 5 6 7 most

HELPFUL: Subject is willing to assist, accommodate, or cooperate with other chimpanzees.

least 1 2 3 4 5 6 7 most

6

BULLYING: Subject is overbearing and intimidating towards younger or lower ranking chimpanzees.

least 1 2 3 4 5 6 7 most

AGGRESSIVE: Subject often initiates fights or other menacing and agonistic encounters with other chimpanzees.

least 1 2 3 4 5 6 7 most

MANIPULATIVE: Subject is adept at forming social relationships for its own advantage, especially using alliances and friendships to increase its social standing. Chimpanzee seems able and willing to use others.

least 1 2 3 4 5 6 7 most

GENTLE: Subject responds to others in an easy-going, kind, and considerate manner. Subject is not rough or threatening.

least 1 2 3 4 5 6 7 most

AFFECTIONATE: Subject seems to have a warm attachment or closeness with other chimpanzees. This may entail frequently grooming, touching, embracing, or lying next to others.

least 1 2 3 4 5 6 7 most

7

EXCITABLE: Subject is easily aroused to an emotional state. Subject becomes highly aroused by situations that would cause less arousal in most chimpanzees.

least most

1 2 3 4 5 6 7

IMPULSIVE: Subject often displays some spontaneous or sudden behavior that could not have been anticipated. There often seems to be some emotional reason behind the sudden behavior.

least most

1 2 3 4 5 6 7

INQUISITIVE: Subject seems drawn to new situations, objects, or animals. Subject behaves as if it wishes to learn more about other chimpanzees, objects, or persons within its view.

least most

1 2 3 4 5 6 7

SUBMISSIVE: Subject often gives in or yields to another chimpanzee. Subject acts as if it is subordinate or of lower rank than other chimpanzees

least most

1 2 3 4 5 6 7

8

COOL: Subject seems unaffected by emotions and is usually undisturbed, assured, and calm.

least most

1 2 3 4 5 6 7

DEPENDENT/FOLLOWER: Subject often relies on other chimpanzees for leadership, reassurance, touching, embracing and other forms of social support.

least most

1 2 3 4 5 6 7

IRRITABLE: Subject often seems in a bad mood or is impatient and easily provoked to anger exasperation and consequent agonistic behavior.

least most

1 2 3 4 5 6 7

UNPERCEPTIVE: Subject is slow to respond or understand moods, dispositions, or behaviors of others.

least most

1 2 3 4 5 6 7

PREDICTABLE: Subject's behavior is consistent and steady over extended periods of time. Subject does little that is unexpected or deviates from its usual behavioral routine.

least most

1 2 3 4 5 6 7

9

DECISIVE: Subject is deliberate, determined, and purposeful in its activities.

least most

1 2 3 4 5 6 7

DEPRESSED: Subject does not seek out social interactions with others and often fails to respond to social interactions of other chimpanzees. Subject often appears isolated, withdrawn, sullen, brooding, and has reduced activity.

least most

1 2 3 4 5 6 7

CONVENTIONAL: Subject seems to lack spontaneity or originality. Subject behaves in a consistent manner from day to day and stays well within the social rules of the group.

least most

1 2 3 4 5 6 7

SENSITIVE: Subject is able to understand or read the mood, disposition, feelings, or intentions of other chimpanzees often on the basis of subtle, minimal cues.

least most

1 2 3 4 5 6 7

10

DEFIANT: Subject is assertive or contentious in a way inconsistent with the usual dominance order. Subject maintains these actions despite unfavorable consequences or threats from others.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

INTELLIGENT: Subject is quick and accurate in judging and comprehending both social and non-social situations. Subject is perceptive and discerning about social relationships.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

PROTECTIVE: Subject shows concern for other chimpanzees and often intervenes to prevent harm or annoyance from coming to them.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

QUITTING: Subject readily stops or gives up activities that have recently been started.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

11

INVENTIVE: Subject is more likely than others to do new things including novel social or non-social behaviors. Novel behavior may also include new ways of using devices or materials.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

CLUMSY: Subject is relatively awkward or uncoordinated during movements including but not limited to walking, acrobatics, and play.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

ERRATIC: Subject is inconsistent, indefinite, and widely varying in its behavior and moods.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

FRIENDLY: Subject often seeks out contact with other chimpanzees for amiable, genial activities. Subject infrequently initiates hostile behaviors towards other chimpanzees.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

ANXIOUS: Subject often seems distressed, troubled, or is in a state of uncertainty.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

12

LAZY: Subject is relatively inactive, indolent, or slow moving and avoids energetic activities.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

DISORGANIZED: Subject is scatterbrained, sloppy, or haphazard in its behavior as if not following a consistent goal.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

UNEMOTIONAL: Subject is relatively placid and unlikely to become aroused, upset, happy, or sad.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

IMITATIVE: Subject often mimics, or copies behaviors that it has observed in other chimpanzees.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

INDEPENDENT: Subject is individualistic and determines its own course of action without control or interference from other chimpanzees.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

13

APPENDIX B9. CHAPTER 7 – BEHAVIOURS

Chimp:		Date:		Time:		Observer:							
Access:		Time of last meal:		All in one go?									
Time	All occurrences (frequency)								Scan on beep (frequency)				Notes
	Other SDB	Regurge	Reingest	Rocking	Scratch	Rub	Yawn	Self groom	Activity	Location	Food?	Mixed?	
:30													
1:00													
1:30													
2:00													
2:30													
3:00													
3:30													
4:00													
4:30													
5:00													
5:30													
6:00													
6:30													
7:00													
7:30													
8:00													
8:30													
9:00													
9:30													
10:00													
TOTAL									Display	1	Y	Y	OOS
									Fight	2	N	N	
									Forage	3			
	TOTAL DURATION								Grm, OTH	Out			
									Grm, REC	RP			
									Grm, SLF				
									Loc				
									Play				
									Rest				
									Sex behav				

APPENDIX C: OBSERVATIONS & SAMPLES

APPENDIX C1: CHAPTER 4 – OBSERVATIONS PER CONDITION

Distribution of observation periods and total durations for each phase of the Research Pod Activity condition outlined in Chapter 4: Initial Training (IT), Self Recognition (SR), and Touchscreen Tasks (TS). The annotation of an asterisk (*) indicates that the chimpanzee did not have enough Qualifying Footage to be included in analyses.

		Husbandry Training			Research Pod Activities			Baseline		
		IT	SR	TS	IT	SR	TS	IT	SR	TS
Cindy	Observations	6	2	1	6	8	8	2	2	1
	Duration (s)	180	180	180	180	180	180	1206	1154	600
David	Observations	6	2	3	6	*	*	2	2	1
	Duration (s)	180	180	180	180	180	180	993	1204	600
Emma	Observations	6	2	4	6	11	14	2	2	1
	Duration (s)	180	180	180	180	180	180	1206	1203	600
Kilimi	Observations	5	2	1	6	7	8	2	2	1
	Duration (s)	180	180	180	180	180	180	1204	1202	240
Kindia	Observations	6	2	2	6	*	*	2	2	1
	Duration (s)	180	180	180	180	180	180	1205	1203	600
Liberius	Observations	6	2	3	6	8	8	2	2	1
	Duration (s)	180	180	180	180	180	180	1204	1208	300
Louis	Observations	5	1	2	6	11	9	2	1	1
	Duration (s)	180	180	180	180	180	180	1239	601	600
Lucy	Observations	*	2	4	6	*	*	1	2	1
	Duration (s)	180	180	180	180	180	180	621	1203	600
Lyndsey	Observations	*	3	*	6	8	*	2	3	1
	Duration (s)	180	180	180	180	180	180	1205	1262	600
Qafzeh	Observations	5	2	3	5	8	9	2	2	1
	Duration (s)	180	180	180	180	180	180	1206	1203	600
Ricky	Observations	6	3	*	4	8	*	2	2	1
	Duration (s)	180	180	180	180	180	180	1204	1204	600

APPENDIX C2: CHAPTER 7 – OBSERVATIONS PER CONDITION

ANALYSES		1a 1b 1c 1d 1e 1f	1a 1b 1c	1a 1b 1c 6a 6c 6d 6f 6g	1a 1b 1c 6a 6d 6g	2a 2c 2e 2f	2a 2c 2e 2f	1a 1b 1c 5 6a 6b 6c 6d 6e 6f 6g 6h 7a 7b 7d	1d 1e 1f 7c 7e	1d 1e 1f 7c 7e	2b 2d 2f 2g						2b 2d 2f 2g						4a 4b 4c		3a 3b 3c					
CHIMPANZEE	Group	Baseline	Pre-introductions	Before Mix	Mix	--Mix-- (removed)	--Mix-- (added)	Integration	--Initial Integration-- 8-27 Jul 2010	--Follow-up Integration-- 8-27 Oct 2010	Removed*						Added						Space (square metres)		Number of rooms					
											2	4	5	6	7	10	9	11	13	16	20	22	0-400	1800-2213	1	2	3	4	5	
Bram	BB	1	1	5	17	3	14	28	6	6					2	1		8	3	1	2	6	23	33	11	17	1	14	13	
Claus	BB	1	1	6	15	14	1	29	6	6		1	11		2							7	23	28	16	7	6	10	12	
Edith	BB	1	1	5	16	15	1	29	6	6		1	11		2	1					1	7	23	28	16	7	5	12	11	
Eva	BB	1	1	5	17	4	16	28	6	6						1	2	8	3	1	2	6	18	33	10	12	3	12	14	
Frek	BB	1	1	6	15	13	2	29	6	6			11		2					1	1	7	22	29	15	7	1	15	13	
Heleen	BB	1	1	6	15	0	15	29	6	6							2	8	3	1	1	7	15	36	9	14	3	10	15	
Lianne	BB	1	1	6	15	0	15	29	6	6							2	8	3	1	1	7	16	35	8	14	3	9	17	
Paul	BB	1	1	5	17	15	2	28	6	6		1	11		2	1					2	6	23	28	14	6	5	10	16	
Pearl	BB	1	1	6	15	0	15	29	6	6						2	8	3	1	1	7	14	37	8	14	2	12	15		
Rene	BB	1	1	5	17	3	14	28	6	6					2	1				1	2	6	17	34	8	16	5	11	11	
Sophie	BB	1	1	6	15	14	1	29	6	6		1	11		2						1	7	23	28	16	7	3	9	16	
Cindy	ED	3	1	6	15	0	15	29	6	6							2	8	3	1	1	7	10	41	6	9	7	13	15	
David	ED	3	1	6	15	0	15	29	6	6							2	8	3	1	1	7	10	41	7	12	3	20	9	
Emma	ED	3	1	6	16	0	16	28	6	6							2	8	3	1	2	6	11	40	6	12	8	15	10	
Kilimi	ED	3	1	6	15	13	2	29	6	6		2		11							1	1	7	13	38	12	9	5	13	12
Kindia	ED	3	1	6	15	14	1	29	6	6		1	2		11							7	14	37	12	9	4	13	13	
Liberius	ED	3	1	6	15	11	4	29	6	6				11					3	1	1	7	14	37	8	10	7	13	13	
Louis	ED	3	1	6	15	0	15	29	6	6							2	8	3	1	1	7	10	41	10	8	7	14	12	
Lucy	ED	3	1	6	15	11	4	29	6	6				11					3	1	1	7	13	38	8	13	5	11	14	
Lyndsey	ED	3	1	5	17	14	3	28	6	6		2		11		1				1	2	6	15	36	10	8	7	13	13	
Qafzeh	ED	3	1	6	16	14	2	28	6	6		1	2		11						2	6	15	36	11	9	7	12	12	
Ricky	ED	3	1	6	15	0	15	29	6	6							2	8	3	1	1	7	9	42	6	13	7	12	13	
n =		22	22	22	22	11	11	22	22	22	2	8	5	6	7	6	9	11	13	16	20	22	22	22	22	22	22	22	22	22

Notes: (1) A total of 8 individuals were included for group size 10 because both groups experienced a group size of 4 during the Mix (individuals removed) phase; (2) Data for R/R only included the BB group, except Analysis 5; (3) Numbers crossed out for Mix subsections were not included in analyses.

APPENDIX C3: CHAPTER 7 – SAMPLE POINTS FOR GROUP SIZE

The number of sample points (for analyses 2b, 2d, and 2f) for each group size varied based on the pace of the introductions. Data were drawn from the following phases: Individuals Removed was from the Mix phase, Individuals Added was from the Mix phase through Initial Integration, and All Sizes was from the Mix through the entire Integration phase. An asterisk (*) indicates that eight individuals were included for group size 4 because both groups were observed (on separate days) when their original group consisted of four chimpanzees. A caret (^) indicates that six individuals were included for group size 10 because four observations were completed prior to the start of that day's introduction and subsequent removal of an individual.

Group Size	SDBs & Allogroom			R/R	
	Individuals Removed	Individuals Added	All Sizes	Individuals Removed	Individuals Added
2	2		2		
4	8*		8*	4	
5	5		5	5	
6	6		6		
7	7		7	7	
9		9	9		4
10	6^		6^	5	
11		11	11		6
13		13	13		6
16		16	16		7
20		20	20		10
22		22	22		11

APPENDIX D: DETAILS FOR CHAPTER 2

APPENDIX D1: CHAPTER 2 – CHIMPANZEE DIET

Details of chimpanzee diet and feeding instructions as of 11 June 2010 (with weight or quantity).

	Vegetables	Fruit	Greens	Misc
Monday		Grapes and mangoes (35kg); Apples (40kg)	Leeks, spring onions, celery (60kg)	Avocados (22)
Tuesday	Broccoli, fennel, peppers (70kg)	Melons and pears (45kg)		Boiled eggs (44)
Wednesday	Sweet potatoes, parsnips, turnips (50kg)	Grapes and mangoes (30kg)	Lettuce, spring greens, kale, spinach (45kg)	Bread (4 loaves)
Thursday	Beetroot, onions, potatoes (45kg)	Apples (40kg); Melons and tomatoes (40kg)		Pulses (4 trays)
Friday	Carrots, sweet potatoes, cauliflower (65kg)	Pears and mangos (50kg)		Boiled eggs (44) and avocados (22)
Saturday		Apples (60kg)	Cucumbers, broccoli, cabbage (55kg)	Cheese (4 blocks)
Sunday	Carrots, onions, turnips, (65kg)	Pears and grapes (50kg)		Bulbs of garlic (22)

- Banana is only to be fed during training sessions, and at no other time. Thirty-five bananas will be delivered daily.
- All food is to be presented in a variety of ways (chopped, whole, etc).
- At least two scatters (1/2 bucket of each) to be provided daily (see Table 2.4).
- One bucket of Trio Munch (primate pellet) to be provided daily
- All food should be split into 5-8 feeds per day.
- Food may be fed in any combination, at any time throughout day, but big feeds just before lunchtime should be avoided, if possible (as this affects afternoon training sessions).
- Fresh browse to be provided as available.
- Greens should be coated in corn oil.

APPENDIX D2: CHAPTER 2 – CHIMPANZEE SCATTER ROTA

Details of chimpanzee scatter rota with food item and weight provided.

Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
Raisins (2.5kg)	Dates (2.5kg)	Popcorn (500g)	Peanuts (2kg)	Raisins (2.5kg)	Popcorn (500g)	Whole nuts (2.5kg)
Sunflower seeds (1.3kg)	Peanuts (2kg)	Sunflower seeds (1.3kg)	Dried fruit (1.5kg)	Flaked maize (1.5kg)	Dates (2.5kg)	Flaked maize (1.5kg)

APPENDIX D3: CHAPTER 2 –FOOD REWARDS

Details of food rewards used in training and research sessions (and frequency of use during sessions). All food rewards were cut into small pieces (e.g. $\frac{1}{4}$ - $\frac{1}{2}$ dried fig, one nut, slice of banana $\frac{1}{2}$ inch thick).

	Dried fruit	Nuts	Banana pieces	Juice
Husbandry training	None	None	Yes (regularly)	Yes (regularly)
Research training & testing	Yes (regularly)	Yes (occasionally)	Yes (rarely)	None

APPENDIX E: DETAILS FOR CHAPTER 4

APPENDIX E1: CHAPTER 4 – VIDEO-CODED DATA (OUT OF SIGHT)

Details for video-coded observations in Chapter 4 which included no more than two seconds of the focal animal being out of sight (i.e. blocked by another chimpanzee or stepped out of view of the camera).

Observation #	Focal animal	Phase	Out of sight (sec)
434	Emma	Self Recognition	2
478	Qafzeh	Self Recognition	2
491	Cindy	Touchscreen Tasks	2
504	Emma	Touchscreen Tasks	2

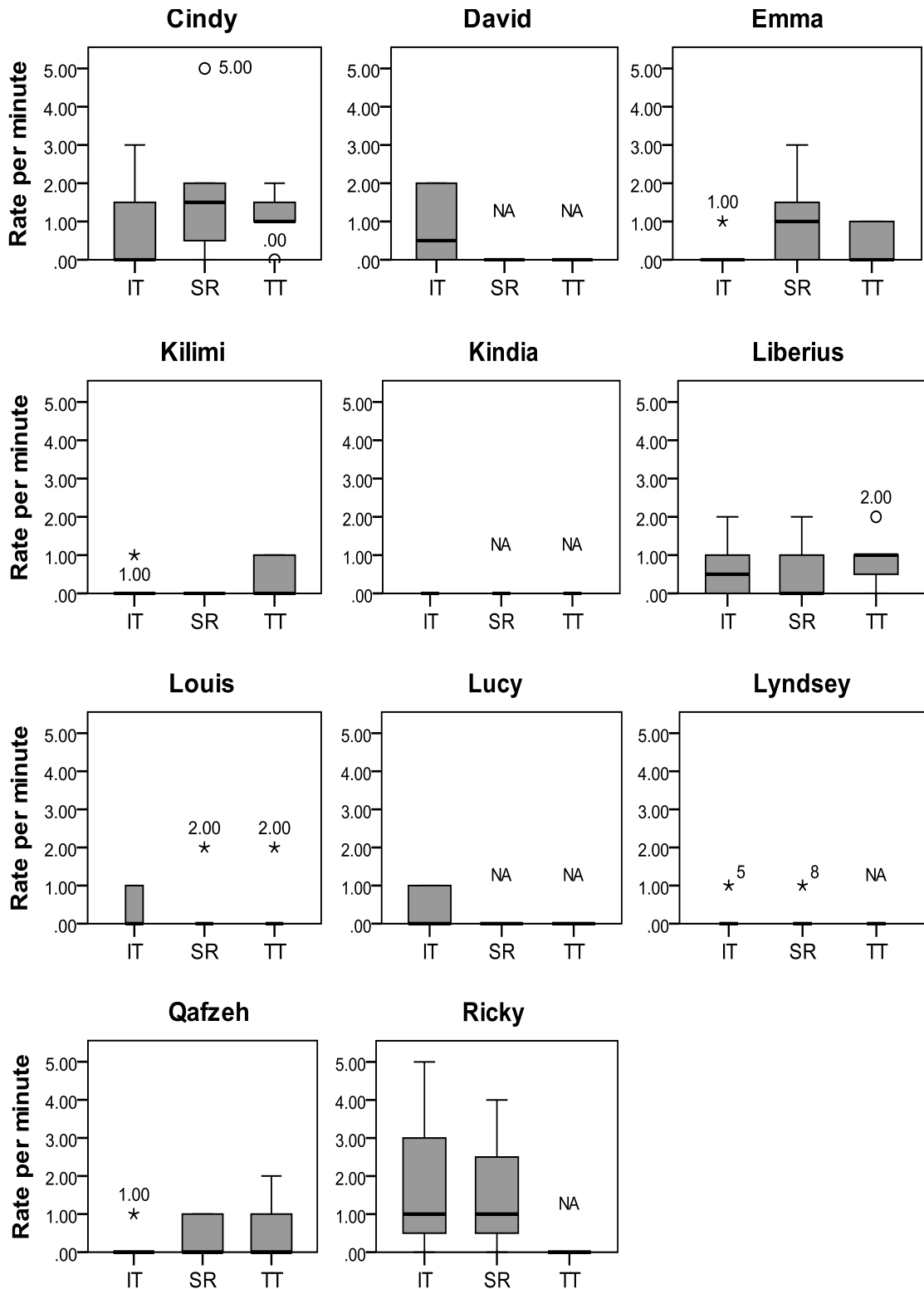
APPENDIX E2: CHAPTER 4 – ANALYSES FOR SCRATCH AND RUB

Additional statistics for Chapter 4 analyses using SDBs to separate the behaviours that were collapsed into the SDB category: scratch and rub. Abbreviations used: B = Baseline, HT = Husbandry Training, and RP = Research Pod. An asterisk (*) indicates significance.

#	Data	Test	n	df	Test Stat	p	Sig Value	Effect Size (r)
1a	Scratch	Friedman's two-way ANOVA (Medians: B = 0.20; HT = 0.61; RP = 0.28)	6	2	$\chi^2 = 7$	0.03*	0.05	
		Wilcoxon signed-rank test (post hoc): B vs HT			$T = 21$	0.03	0.0167	0.9
		Wilcoxon signed-rank test (post hoc): B vs RP			$T = 16$	0.25	0.0167	0.47
		Wilcoxon signed-rank test (post hoc): HT vs			$T = 6$	0.35	0.0167	-0.38
	Rub	Friedman's two-way ANOVA (Medians: B = 0.31; HT = 0.39; RP = 0.78)	6	2	$\chi^2 = 7.91$	0.02*	0.05	
		Wilcoxon signed-rank test (post hoc): B vs HT			$T = 16$	0.25	0.0167	0.47
		Wilcoxon signed-rank test (post hoc): B vs RP			$T = 21$	0.03	0.0167	0.9
		Wilcoxon signed-rank test (post hoc): HT vs			$T = 14$	0.08	0.0167	0.72
1b	Scratch	Friedman's two-way ANOVA (Medians: B = 0.40; HT = 1.0; RP = 0.33)	9	2	$\chi^2 = 6.65$	0.04*	0.05	
		Wilcoxon signed-rank test (post hoc): B vs HT			$T = 35$	0.017	0.0167	0.79
		Wilcoxon signed-rank test (post hoc): B vs RP			$T = 15$	0.67	0.0167	-0.14
		Wilcoxon signed-rank test (post hoc): HT vs			$T = 6.5$	0.20	0.0167	-0.42
	Rub	Friedman's two-way ANOVA (Medians: B = 0.19; HT = 0.33; RP = 0.33)	9	2	$\chi^2 = 1.27$	0.53	0.05	
1c	Scratch	RM ANOVA (Transformed – Mean, SE: B = 0.24, 0.14; HT = 0.46, 0.25; RP = 0.40, 0.17)	6	2, 10	$F = 1.17$	0.35	0.05	
	Rub	RM ANOVA (Mean, SE: B = 0.50, 0.14; HT = 0.89, 0.32; RP = 1.06, 0.16)	6	2, 10	$F = 2.21$	0.16	0.05	
2a	Scratch	T-test (Transformed – Mean, SE: Alone = 0.30, 0.19; Others = 0.41, 0.22)	6	5	$t = -0.45$	0.68	0.05	0.20
	Rub	Wilcoxon signed-rank test (Medians: Alone = 0.72; Others = 0.43)	6		$T = 8$	0.89	0.05	0.06
4	Scratch	T-test (Mean, SE: Contingent = 0.47, 0.25; Not contingent = 0.89, 0.58)	6	5	$t = -1.11$	0.32	0.05	0.45
	Rub	T-test (Mean, SE: Contingent = 0.78, 0.13; Not contingent = 0.89, 0.32)	6	5	$t = -0.2$	0.85	0.05	0.09
6	Scratch	T-test (Transformed – Mean, SE: Visual = 0.55, 0.14; No visual = 0.93, 0.18)	6	5	$t = -2.17$	0.08	0.05	0.70
	Rub	T-test (Mean, SE: Visual = 0.50, 0.14; No visual = 0.97, 0.21)	6	5	$t = -2.10$	0.9	0.05	0.68
7c	Scratch	Spearman's correlation coefficient: IT scratch (Median = 0.33)	11		$r = -0.13$	0.71	0.05	
		Spearman's correlation coefficient: ALL scratch	6		$r = 0.37$	0.47	0.05	
	Rub	Spearman's correlation coefficient: IT rub (Median = 0.33)	11		$r = 0.24$	0.47	0.05	
		Spearman's correlation coefficient: ALL rub (Median = 0.78)	6		$r = -0.12$	0.82	0.05	

APPENDIX E3: CHAPTER 4 – INDIVIDUAL SDB SCORES

Median and IQR of SDB rate per minute for each individual across Research Pod Activities. IT = Initial Training; SR = Self Recognition; TS = Touchscreen Tasks. Whiskers represent 5th and 95th percentile, circles and stars show outliers, and numbers represent the corresponding data point. Graphs of those who did not having enough Qualifying Footage for any phase were marked with NA.



APPENDIX F: DETAILS FOR CHAPTER 5

APPENDIX F1: INFORMED CONSENT AND RATING SCALE (TWO-SIDED LAMINATED A4 CARD)

The Chimpcam Project

- This survey is anonymous. Your data will be treated with full confidentiality and if published, will not be identifiable as yours.
- We ask for your honesty on all of the questions, but please note that you may omit any question you are not comfortable with, or choose to stop the survey at any time, for any reason.
- Your completion of the study serves as your voluntary agreement to participate in the research.

The Chimpcam Project

1	2	3	4	5
Strongly Disagree	Slightly Disagree	Neither Agree nor Disagree	Slightly Agree	Strongly Agree

APPENDIX F2: DEBRIEFING (TWO-SIDED BUSINESS CARD)



Thank you for participating in our survey!

Objective: Find out what impact the broadcast of a documentary about the chimps of Budongo Trail and cognition has on the public.

Researcher email: elizabeth.herrelko@stir.ac.uk

www.chimpcam.com

APPENDIX F3: WEATHER REPORTED DURING THE STUDY

Date	Weather	Temperature (C)	Humidity
20 Jan (Wed)	Overcast with rain	3	84%
21 Jan (Thur)	Partly cloudy with rain	4	80%
23 Jan (Sat)	Overcast with rain	2	94%
24 Jan (Sun)	Overcast with rain	3	93%
25 Jan (Mon)	Overcast	3	80%
26 Jan (Tue)	Overcast	2	88%
27 Jan (Wed)	Partly cloudy	8	80%
28 Jan (Thur)	Partly cloudy with rain	4	85%
29 Jan (Fri)	Sunny	2	68%
30 Jan (Sat)	Sunny	0	72%
31 Jan (Sun)	Sunny	1	75%
1 Feb (Mon)	Partly cloudy	0	84%
2 Feb (Tue)	Overcast with snow	0	89%
3 Feb (Wed)	Overcast	-4	88%
4 Feb (Thur)	Overcast	2	90%
5 Feb (Fri)	Overcast	6	89%
6 Feb (Sat)	Overcast with rain	5	94%
7 Feb (Sun)	Overcast with rain	4	92%

APPENDIX F4: IOR DURING THE STUDY

IOR between the researcher and volunteers recording visitors to Budongo Trail.

Volunteer	Group size		Adults		Children 12 & under		Children 13-18	
	p	n	p	n	p	n	P	n
Alexis	1.0	2	1.0	2	1.0	2	1.0	2
Allyson	1.0	8	1.0	8	1.0	8	1.0	8
Amanda	1.0	3	1.0	3	1.0	3	1.0	3
Anne	1.0	5	1.0	5	1.0	5	1.0	5
Ciara	0.99	8	1.0	8	0.96	8	1.0	8
David	1.0	5	1.0	5	0.90	5	1.0	5
Elaine	1.0	10	0.96	10	0.87	10	0.87	10
Esther	1.0	12	0.77	12	0.96	12	1.0	12
Fiona	0.97	21	0.95	21	0.84	21	1.0	21
Helen	0.93	19	0.80	19	0.93	19	1.0	19
James	1.0	5	1.0	5	0.9	5	1.0	5
Norman	1.0	5	1.0	5	0.9	5	1.0	5
Pat	1.0	4	1.0	4	1.0	4	1.0	4
Peter	1.0	4	1.0	4	1.0	4	1.0	4
Rae	0.98	10	1.0	10	0.97	10	1.0	10
Rhona	1.0	2	1.0	2	1.0	2	1.0	2
Therese	1.0	8	1.0	8	1.0	8	1.0	8

APPENDIX G: DETAILS FOR CHAPTER 6

APPENDIX G1: MULTIPLE REGRESSION RESULTS MATRIX

Significant models from 105 paired combinations per category: visual access (0), personality profiles (12), and video introductions (9).

Outcome		Visual Access					Personality Profiles					Video Introductions				
Introduced to	Behaviour	All	F	M	High	Low	All	F	M	High	Low	All	F	M	High	Low
All	AGG											X				
	AFF											X				
	NEU											X				
Females	AGG															
	AFF						X									
	NEU						X		X					X		
Males	AGG						X					X		X		
	AFF															
	NEU						X									
High Ranks	AGG															
	AFF														X	
	NEU															
Low Ranks	AGG															
	AFF						X									
	NEU						X	X				X				
In-group (All)	AGG										X	X				
	AFF															
	NEU						X									
Out-group (All)	AGG						X									
	AFF															
	NEU						X									

APPENDIX G2: INTRACLASS CORRELATION COEFFICIENTS

(A) The 54 personality variables included in the Hominoid Personality Questionnaire.

Traits	Edinburgh Raters		Beekse Bergen Raters	
	ICC (3, 1)	ICC (3, k)	ICC (3, 1)	ICC (3, k)
Active	0.64	0.88	0.62	0.87
Affectionate	0.12	0.35	0.20	0.50
Aggressive	0.82	0.95	0.25	0.58
Anxious	0.18	0.47	0.77	0.93
Autistic	0.61	0.86	0.58	0.85
Bullying	0.82	0.95	0.06	0.20
Cautious	0.11	0.33	0.39	0.72
Clumsy*	0.10	0.30	-0.14	-1.02
Conventional	0.03	0.09	0.38	0.71
Cool	0.31	0.65	0.32	0.65
Curious	0.25	0.58	0.27	0.60
Decisive	0.23	0.54	0.70	0.90
Defiant	0.53	0.82	0.50	0.80
Dependent	0.40	0.73	0.40	0.73
Depressed	0.20	0.50	0.54	0.83
Disorganized	0.16	0.43	0.42	0.74
Distractible	0.45	0.77	0.50	0.80
Dominant	0.85	0.96	0.58	0.85
Erratic	0.34	0.68	0.22	0.53
Excitable	0.11	0.33	0.46	0.77
Fearful	0.41	0.73	0.56	0.83
Friendly*	-0.12	-0.79	0.07	0.23
Gentle	0.56	0.84	0.65	0.88
Helpful*	0.29	0.62	-0.06	-0.29
Imitative	0.47	0.78	0.26	0.58
Impulsive*	0.11	0.32	-0.19	-1.79
Independent	0.25	0.57	0.85	0.96
Individualistic*	0.23	0.54	-0.27	-5.67
Innovative	0.58	0.85	0.43	0.75
Inquisitive	0.40	0.72	0.59	0.85
Intelligent	0.53	0.82	0.22	0.53
Inventive	0.60	0.86	0.58	0.84
Irritable*	0.32	0.66	-0.04	-0.19
Jealous	0.23	0.55	0.10	0.31
Lazy*	0.65	0.88	-0.17	-1.44
Manipulative	0.43	0.75	0.15	0.42

Traits	Edinburgh Raters		Beekse Bergen Raters	
	ICC (3, 1)	ICC (3, k)	ICC (3, 1)	ICC (3, k)
Persistent	0.16	0.44	0.37	0.70
Playful	0.45	0.77	0.41	0.74
Predictable*	0.07	0.24	-0.13	-0.86
Protective	0.59	0.85	0.56	0.83
Quitting	0.28	0.61	0.57	0.84
Reckless	0.52	0.81	0.18	0.47
Sensitive*	0.13	0.38	-0.14	-0.94
Sociable	0.29	0.62	0.46	0.78
Solitary	0.80	0.94	0.50	0.80
Stable	0.11	0.33	0.32	0.65
Stingy/Greedy	0.47	0.78	0.20	0.50
Submissive	0.77	0.93	0.68	0.90
Sympathetic	0.34	0.67	0.53	0.82
Thoughtless*	0.20	0.50	-0.02	-0.09
Timid	0.61	0.86	0.75	0.92
Unemotional	0.49	0.79	0.32	0.65
Unperceptive	0.22	0.54	0.40	0.73
Vulnerable	0.16	0.44	0.41	0.73

Note: An asterisk (*) denotes omitted items due to low IOR.

(B) The Physical Introduction ratings for multiple observers: the researcher and three keepers.

	ICC (3,1)	ICC (3,k)
Aggressive	699.39	0.95
Affiliative	197.50	0.31
Submissive*	1085.26	-0.03
Neutral	1792.58	0.83

Note: An asterisk (*) denotes omitted items due to low IOR.

APPENDIX H: INTRODUCTION TIMELINE

Type	Date	Party A	Party B	Notes		
Auditory Access	Chapter 7 - Preintroductions)	18-Mar-10	All	All	Edinburgh in Pods 1, 3, and outside; Beekse Bergen in Pod 2.	
		19-Mar-10	All	All	Edinburgh in Pods 1, 3, and outside; Beekse Bergen in Pod 2.	
		20-Mar-10	All	All	Edinburgh in Pods 1, 3, and outside; Beekse Bergen in Pod 2.	
		21-Mar-10	All	All	Edinburgh in Pods 1, 3, and outside; Beekse Bergen in Pod 2.	
		22-Mar-10	All	All	Edinburgh in Pods 1, 3, and outside; Beekse Bergen in Pod 2.	
		23-Mar-10	All	All	Edinburgh in Pods 1, 3, and outside; Beekse Bergen in Pod 2.	
Video Introductions 1						
Visual Access	Chapter 7 - Preintroductions)	24-Mar-10	Visual access	All	100 minutes.	
		26-Mar-10	Visual access	All	90 minutes.	
		Video Introductions 2				
		27-Mar-10	Visual access	All	All	5 hours.
		28-Mar-10	Visual access	All	All	5 hours.
		29-Mar-10	Visual access	All	All	5 hours.
Video Introductions 3						
		30-Mar-10	Visual access	All	Overnight, separated by two layers of mesh (i.e. middle bed empty).	

Type	Date	Party A	Party B	Notes	
Physical introductions: Preliminary (Chapter 7 - Before Mix)	31-Mar-10	Louis	Eva, Heleen	50 minutes. Separated by mesh.	
		Louis	Heleen	25 minutes. Physical contact.	
		Louis	Pearl	32 minutes. Physical contact.	
	01-Apr-10	Louis	Heleen	30 minutes. Separated by mesh, then physical contact.	
	02-Apr-10	Louis	Sophie	40 minutes. Separated by mesh, then physical contact.	
		<i>add:</i>	Pearl	13 minutes. Separated by mesh, then physical contact.	
	05-Apr-10	Paul	Cindy	27 minutes. Separated by mesh. Avoidance behaviours from both.	
	Period of no introductions due to additional quarantine measures and injured chimpanzees.				
	20-Apr-10	Visual access	All		Overnight, separated by two layers of mesh
	21-Apr-10	Visual access	All		Overnight, separated by two layers of mesh.
	Video Introductions 4				
	22-Apr-10	Visual access	All		Overnight, separated by two layers of mesh.
	22-Apr-10	Visual access	All		Overnight, separated by two layers of mesh.
	26-Apr-10	Louis	Pearl		40 minutes.
		Visual access	All		Overnight, separated by two layers of mesh.
	27-Apr-10	Visual access	All		
	28-Apr-10	Kindia	Paul		30 minutes. Mesh (2 layers, then one with contact through mesh).
	Video Introductions 5				
	29-Apr-10	Louis	Pearl		
	30-Apr-10	Visual access	All		Overnight separated by two layers of mesh.
	01-May-10	Visual access	All		Overnight, separated by two layers of mesh.
	02-May-10	Visual access	All		Overnight, separated by two layers of mesh.
	05-May-10	Visual access	All		Overnight, separated by two layers of mesh.
	Video Introductions 6				
	10-May-10	Visual access	All		Overnight, separated by two layers of mesh.
	Video Introductions 7				

Type	Date	Party A	Party B	Notes	
Physical introductions: "Super group" (Chapter 7 - Mix)	1	12-May-10	Louis	Pearl	Start of "super group".
	2	16-May-10	Heleen	David	2 hours.
			<i>add:</i> Louis, Pearl		2 hours, then sent to "super group" enclosure.
	Video Introductions 8				
	3	24-May-10	Emma, Cindy	Eva, Lianne	Overnight, no mesh.
		25-May-10	<i>add:</i> Louis, David, Heleen, Pearl		Sent to "super group" enclosure.
	4	26-May-10	Ricky	Heleen, David, Louis	Through mesh for first minute, then physical contact.
			<i>add:</i> Pearl, Lianne, Eva		Through mesh briefly, then physical contact.
			<i>add:</i> Cindy, Emma		Through mesh for 4 minutes, physical contact with entire "super group", then sent to "super group" enclosure.
	Video Introductions 9				
	5	01-Jun-10	Bram, Rene	Louis, David	Overnight, separated by one layer of mesh.
		02-Jun-10	<i>add:</i> rest of "super group"		Sent to "super group" enclosure.
	Video Introductions 10				
	6*	09-Jun-10	Lucy, Liberius	Louis, Pearl, Lianne, Eva	Separated by mesh and returned to groups after 2 hours.
	7*	16-Jun-10	Lyndsey, Liberius	Edith, Sophie	Attempt aborted due to difficulties shifting chimps.
	8	21-Jun-10	Lucy, Liberius	Cindy	
			<i>add:</i> Eva, Lianne, Pearl		Overnight, separated by one layer of mesh.
		23-Jun-10	Lucy, Liberius, Cindy	Eva, Lianne, Pearl	Reintroduced in the morning, after a while, Eva and Pearl were swapped with David, Bram, and Rene. (Pearl was removed because Liberius was aggressive towards her.)
David, Bram, Rene			Lianne	David, Bram, and Rene were first reintroduced to Lianne.	
<i>add:</i> Lucy, Liberius, Cindy		Sent to "super group" enclosure.			

Type	Date	Party A	Party B	Notes	
Physical introductions: "Super group" (Chapter 7 - Mix)	9	29-Jun-10	Lyndsey, Kilimi	David	Occurred at the same time in adjacent beds.
			Frek	Rene, Heleen	
			<i>continue:</i> previous 6 together		
			<i>add:</i> Louis, Eva, Lianne		
			<i>add:</i> Ricky, Emma		Sent to "super group" enclosure.
	10	30-Jun-10	Sophie, Edith	Rene, Eva, Pearl, Lianne	
			<i>add:</i> Louis, Bram		Sent to "super group" enclosure.
	11*	01-Jul-10	Qafzeh, Kindia	Louis, David, Rene	Mesh, then physical contact. Too aggressive, chimps were separated, and introduction attempt was aborted.
	12*	01-Jul-10	Qafzeh, Kindia	Paul, Claus	Overnight, separated by one layer of mesh.
		02-Jul-10	Qafzeh, Kindia	Paul, Claus	Overnight, separated by one layer of mesh.
		03-Jul-10	Qafzeh, Kindia	Paul, Claus	Overnight, separated by one layer of mesh.
		04-Jul-10	Qafzeh, Kindia	Paul, Claus	Overnight, separated by one layer of mesh.
	13	05-Jul-10	Qafzeh	Paul	Previous combination failed; try with new combination.
			<i>add:</i> Louis, Eva, Pearl		
			<i>add:</i> Emma, David, Bram		Sent to "super group" enclosure.
	14	07-Jul-10	Kindia	Claus	Overnight, separated by one layer of mesh.
			Kindia	Claus	Separated by one layer of mesh, then physical contact
			<i>add:</i> Louis, David, Paul, Edith, Sophie, Eva, Cindy		
<i>add:</i> Lianne, Lyndsey, Ricky				Doors opened to indoor pods, then to entire enclosure.	

Notes: (1) Only 5 Visual Access days included in the analysis due to lack of data for the 6th day.

(2) Unless otherwise noted, visual access was provided overnight throughout the introduction process when the "super group" was in development.

(3) An asterisk (*) denotes an unsuccessful introduction.