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Spatial and social influences on the behaviour of captive chimpanzees

Luke Mangaliso Duncan

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

Johannesburg 2012

Declaration

I declare that this thesis is my own unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



Luke Mangaliso Duncan

14th day of May 2012

Abstract

Captive animals are frequently subject to imposed, uncontrollable stressors to which they respond through behavioural flexibility, or, failing which, exhibit pathology. Chimpanzees provide an intriguing model to examine how captive environments influence the responses of animals to stress. My study investigates the responses of a group of chimpanzees to imposed stressors of captivity at the Johannesburg Zoo, South Africa. My study comprised four components. Firstly, I examined the effects of spatial restriction on chimpanzee behaviour with regard to an enclosure enlargement, testing several existing models of coping with spatial crowding and another model, based on the coping hypothesis of abnormal behaviour. Behavioural observations of the chimpanzees in their indoor and outdoor exhibits before, during, immediately after and 10 weeks after the enclosure reconstruction revealed that the chimpanzees used tension-reduction and conflict-avoidance tactics as a means to cope with spatial crowding. Moreover, abnormal behaviour appears to provide an outlet for stress under crowding. Secondly, I assessed the long-term effects of past spatial environments on the space use and group spacing of the chimpanzees, five years after the enclosure change. Through behavioural observations and mapping the locations of individuals, I found that the chimpanzees exhibit space-use bias and limited group spacing, contingent on the dimensions of the old enclosure that were not explained by factors such as social or thermal conditions and zoo visitor effects. I propose that the spacing patterns may be due to spatial learned helplessness. Thirdly, I examined the effect of two social manipulations, mandated by zoo management, on the behaviour and socio-dynamics of the chimpanzees. The chimpanzees responded to social change through selective social interactions and non-social behavioural responses suggest that removing an individual was less stressful than the merging of two groups. Finally, I investigated the role of shade as a thermoregulatory resource for captive chimpanzees. Individuals used shade frequently despite observations taking place during the austral winter period, suggesting that shade is a valuable thermal resource for chimpanzees. In conclusion, the chimpanzees responded to most imposed stressors (spatial crowding, social change and thermal stress) through behavioural flexibility, implying successful coping, but failed to cope with previous spatial restrictions, resulting in limited space-use behaviour.

Dedication

For my family, I love you all more than words can express

“The most exciting phrase to hear in science, the one that heralds new discoveries, is not 'Eureka!' but 'That's funny...' ”

Isaac Asimov

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Chapter 1. Introduction

Rationale for my study

My research was started at the Johannesburg Zoo with the aim of investigating how spatial and social factors influence the behaviour of chimpanzees in the context of the zoo environment. My project was part of the ChimpanZoo research program started in 1984 by the Jane Goodall Institute (JGI) with the goal "to increase public awareness about the plight of chimpanzees and to increase understanding of chimpanzee behavior", "to assist zoos in their efforts to improve the habitats and conditions for captive chimpanzees" and "to facilitate the exchange of information on ways to enrich the lives of captive chimpanzees" (www.chimpanzoo.org). In alignment with the goals of ChimpanZoo, and under the mandate of the JGI South Africa, all the studies described in this thesis were 'natural experiments' in the sense that maintenance conditions and husbandry protocols at the Johannesburg Zoo dictated the conditions and changes that took place. As a consequence, I have used the opportunities presented by the changes in the spatial and social environment in the chimpanzee exhibit imposed by management at the Johannesburg Zoo to examine the influences of changes in environmental conditions, and the associated stressors, on the behaviour of captive chimpanzees. Below, I provide a background relevant to the objectives and aims of my thesis including the captive environment, the degree of control available to animals in captivity, imposed stress and animals responses to stress.

The captive environment

Mason (2010) estimates that there are approximately 26 billion animals maintained in captive environments, ranging from invertebrates (Anderson & Wood, 2001) to non-human primates (for this chapter, and the thesis as a whole, I hereafter refer to non-human primates as 'primates', unless explicitly stated as otherwise; Kessel & Brent, 1998). Animals are maintained in captivity for various reasons, including companionship (van Hoek & Cate, 1998; Soulsbury *et al.*, 2009), food (Beattie *et al.*, 1993; Gygax *et al.*, 2007; Keeling, 1995), conservation (Hogan *et al.*, 1988), education and research (Abou-Ismail *et al.*, 2008). The conditions under which captive animals live depend largely on the reasons for their captivity

and the costs associated with their maintenance, but range from small, relatively barren cages (Line *et al.*, 1990) to large, naturalistic, enriched enclosures (Little & Sommer, 2002) with varying social conditions. Even with all the contextual variation that characterises captivity, two underlying characteristics are common to all captive settings: they lack the dynamicity and controllability of the natural environment.

By its very nature, captivity cannot replicate the natural environment (Drickamer, 1973), since it lacks the uncertainty (Clarke & Mayeaux, 1992) and daily challenges (Platt & Novak, 1997) of the natural environment. Free-ranging animals encounter an environment that is variable, complex and dynamic (Platt & Novak, 1997) while captive animals face a relatively homogenous environment, subject to the same conditions day after day. Even highly enriched environments, which typically recreate both aesthetic and functional aspects of the natural environment (Little & Sommer, 2002), cannot fully replicate the natural setting (Almli & Burghardt, 2006) because many aspects of the natural environment cannot be reproduced in captivity. For example, it is difficult to replicate the natural diet of gorillas *Gorilla sp.* (Lukas *et al.*, 1999) or replicate the dynamics of fission-fusion social groups (Clubb & Mason, 2007) in chimpanzee *Pan troglodytes* society (Rowe, 1996; Dunbar & Barrett, 2000).

Level of self-determination and control by animals in captivity

An animal determines how it experiences the environment through its ability to choose between alternatives (Buchanan-Smith & Badihi, 2011) hereafter referred to as control. While the natural environment is not controllable by animals *per se*, the relative degree of control afforded free-living animals is greater than in captivity. Free-living animals can determine what food they eat (Hiramatsu *et al.*, 2009), the habitats they occupy (Mochizuki & Murakami, 2011), the thermal conditions they experience (Barrett *et al.*, 2004; Kosheleff & Anderson, 2009) and the social environment in which they live (Itani, 1977), within the broad constraints imposed by territoriality (Gordon, 1997) and predation risk (Welton *et al.*, 2003). Thus, animals have direct control over their access to resources and through this, ultimately, their success within the natural environment.

In contrast, caregivers determine the environments of captive animals, with almost all environmental conditions imposed on them. The diet of animals is determined by what (Das *et al.*, 2010), when (Baker & Easley, 1996) and how (Ben-Ari, 2001) food is provided by caregivers. The mode of feeding is determined by caregivers as many natural behaviours, such as hunting, are not ‘desirable’ in captivity (Ben-Ari, 2001) and are thus not permitted.

Humans determine the seasonal, climatic and thermal conditions which captive animals experience (Nieuwenhuijsen & de Waal, 1982; Lindburg, 1998; Little & Sommer, 2002), the amount of space provided (Line *et al.*, 1990) and the physical characteristics of the space in which captive animals live. Animals are known to have distinct preferences for the type of enclosure in which they are housed (Chamove & Rohrhuber, 1989; Pines *et al.*, 2007), but are often forced into enclosures simply because it is convenient for caregivers or part of a daily routine. Captive animals have no choice over the social conditions in which they live and are often subject to unnatural groupings or social isolation (Morgan & Tromborg, 2007). Some captive environments, such as zoo environments, expose animals to frequent close contact with people (Mallapur *et al.*, 2005), often with little or no opportunities for animals to hide (reviewed in Fernandez *et al.*, 2009).

Many aspects of biological functioning (e.g. reproduction) are also determined by caregivers. For example, access to mates is predetermined through social manipulations (Price & Stoinski, 2007) or limitations on animal numbers, such that mating is non-random. Reproductive physiology and sexual receptivity are often managed through the use of hormonal implants (Gimenez *et al.*, 2009) or sterilization (Fail *et al.*, 2000), and even growth and development of captive animals is under human control (Preston, 1999).

Environmental enrichment (a broad term referring to a wide range of interventions in captive environments; hereafter referred to as enrichment) is believed to provide animals with some degree of determination through choice, providing behavioural opportunities that are not necessarily otherwise present (Swaisgood & Shepherdson, 2005). There are five common modes of enrichment in captive environments: feeding enrichment, social enrichment, provision of novel objects or toys, training and physical environmental modification (Hurme *et al.*, 2003). While enrichment is generally held to be beneficial (Almli & Burghardt, 2006), each enrichment technique offers different degrees of control for animals. Some enrichment protocols, such as providing destructible objects (chimpanzees: Brent & Stone, 1998; Videan *et al.*, 2005; Sprague-Dawley rats: Belz *et al.*, 2003; Orange-winged Amazon parrots *Amazona amazonica*: Meehan & Mench, 2002), offer a degree of control by allowing animals to manipulate and alter objects as they choose while other protocols, such as training, are designed to direct and manipulate animals into a particular form of behaviour (chimpanzees: Bloomsmith *et al.*, 1994; non-human primates - reviewed in Bloomsmith *et al.*, 2007; Giant panda *Ailuropoda melanoleuca*: Bloomsmith *et al.*, 2003) effectively eliminating the ability of the animal to determine what behaviour is expressed (but see Bayne, 2003).

Animals in captivity cannot determine where, when and how they receive enrichment. Not all enrichment is effective (Van de Weerd *et al.*, 1997), suggesting that many enrichment protocols are not appropriate for particular species or settings. Enrichment should be designed around the biological needs of the organism (Meehan & Mench, 2002; Wells, 2009) but protocols are typically applied in a 'trial-and-error' fashion (van Hoek & Cate, 1998) or protocols are transferred from one species to another without assessing the relevance of the enrichment (Wells *et al.*, 2007). Animals have distinct preferences for the types of enrichment they engage with (Bracke, 2007) but caregivers typically provide enrichment that they think is appropriate. Species-typical psychological factors may also override any control-related benefits of enrichment. For example, because chimpanzees are easily distracted by multiple objects (Tomonaga, 2002), providing objects one at a time may allow chimpanzees to engage with each object more effectively (Brent & Stone, 1998). In contrast, for most other species multiple destructible or manipulatable enrichment objects are provided (e.g. Rozek & Millam, 2011) as these offer individuals the choice of what to engage with and thereby provides a degree of determination (Kessel & Brent, 1998).

Controllability and stress

When an animal perceives a situation or stimulus as being uncontrollable, it will be stressed (Clark *et al.*, 1997). As a result, many aspects of the captive environment are perceived as being stressful for animals (reviewed in Morgan & Tromborg, 2007) and some suggest that on a continuum of environments in which animals can survive, captivity may present an extreme environment on account of the "pressures" [sic] and stressors present in captivity (Rowell, 1967; Judge & de Waal, 1993). Stress in captivity can present challenges to the immune, autonomic nervous system and activation of the hypothalamic-pituitary-adrenal axis (HPA). Glucocorticoids released by the HPA in turn inhibit reproduction, growth and immune functioning, mobilize energy reserves and alter behaviour (Romero *et al.*, 2009) as a means of short-term allostatic restoration (*sensu* McEwen & Wingfield, 2003; Clark *et al.*, 1997).

If the stressor is acute and the environment permits, animals may modify their behaviour as a means of coping (Clark *et al.*, 1997). Behavioural variation in nature allows animals to better cope with change (Koolhaas *et al.*, 2010) and undoubtedly performs a similar function in captivity. However, a successful response is contingent upon animals possessing the inherent flexibility to respond, an idea formalised in the adaptive calibration model of stress response (Del Giudice *et al.*, 2011). The ability to utilize such a response has

consequences for captive animal survival and welfare. For example, generalist species cope better with captivity than specialist species as they are more likely to possess the flexibility to respond in this fashion (Clubb & Mason, 2007; Mason, 2010). Under unnatural conditions, this response type may also drive the development of novel or innovative behaviours (Kummer & Goodall, 1985).

However, failure to react through behavioural plasticity or exposure to chronic stress and the associated HPA activation can reduce reproductive success (Braastad, 1998) and generate pathology (Clark *et al.*, 1997), particularly for highly intelligent species such as primates (van Hoek & Cate, 1998; Honess & Marin, 2006). Chronic HPA activation can induce a variety of somatic pathologies including neurological change (Tamashiro *et al.*, 2005), induced cardiac arrhythmia (Sgoifo *et al.*, 1999) and immunosuppression (Fast *et al.*, 2008). Chronic stress also influences psychology and cognition through altered reactivity to noxious stimuli (Armario *et al.*, 2008), impaired memory acquisition (Zerbib & Laborit, 1990; Ohl & Fuchs, 1999), altered cognitive functioning (reviewed in Mendl, 1999) and emotional disturbances, including frustration, anxiety, depression and helplessness (Fox, 1984). Given the effects of stress on brain function, it is not surprising that many abnormal behaviours are also associated with chronic stress including self-injurious behaviour (Rommeck *et al.*, 2009), coprophagy (Beerda *et al.*, 1999), stereotypic behaviour (Engel *et al.*, 2011) and hair-plucking (reviewed in Reinhardt, 2005).

There is considerable debate regarding the significance, mechanisms and functions of abnormal behaviour. Humans report lower quality of life on account of behavioural pathology (Jenkins *et al.*, 2011), suggesting that the pathology itself is distressing. This is undoubtedly true of many abnormal stress-related pathologies (such as severe self-injurious behaviour; Reinhardt & Rossell, 2001). In this manner, distress and abnormal behaviour may act as a positive feedback, reinforcing the original stressor. Alternatively, such pathology may reflect underlying neuronal dysfunction (Dantzer, 1991), a compensation for a lack of environmental stimuli (Walsh *et al.*, 1982) and an alternative strategy for coping with the increased allostatic load (Rushen, 1993). However, regardless of mechanism or function, abnormal behaviours, and indeed all stress-related pathologies, can act as reliable indicators of stress and wellbeing (Altman, 1999) and undermine good welfare (Li *et al.*, 2007).

Zoos are multi-functional institutions, serving a conservation, research, recreational and educational role (Anderson *et al.*, 2003). Poor animal welfare in captivity, as outlined above, undermines the functioning of zoos on all levels and therefore there is a need for a better understanding of how animals respond to the imposed conditions of zoo environments.

Primates are arguably one of the most popular groups exhibited in zoos, with thousands of primates housed worldwide (Wells, 2005). According to the International Species Information System (ISIS: www.isis.org), approximately 4650 apes are housed in captivity, over a third of which are chimpanzees, but even these numbers are likely to be an underestimation. Chimpanzees are popular animals in zoos and research because of their similarity to humans (Brent & Stone, 1998) but many aspects of chimpanzee biology and behaviour make chimpanzees intriguing subjects to examine the effects of the captive environment on animals.

My study concerns investigating how chimpanzees respond to changes in space and the social and physical circumstances imposed on them at the Johannesburg Zoo. These changes took place over varying time frames, which represent short term (possibly acute) and long term (possibly chronic) stressors to the chimpanzees. Investigating how chimpanzees respond to these stressors both contributes to our understanding of how an intelligent and iconic species copes with imposed environmental stress as well as our assessments of the welfare of captive chimpanzees.

Study species

Description

Chimpanzees are large black primates, ranging in body length from approximately 730-960mm (Rowe, 1996), with males weighing between 43-60kg and females between 34-46kg (Dunbar & Barrett, 2000). Breeding primarily occurs during October and November, but is known to occur year round (Rowe, 1996). Chimpanzees signal ovulation through large pink anogenital swellings (Dunbar & Barrett, 2000), have an oestrus cycle lasting 36 days, a gestation period of 240 days and a mean birth interval of 60 months (Rowe, 1996). Chimpanzees are social, living in complex, multi-male, multi-female, fission-fusion troops comprising between 20 and 100 individuals (Wallace, 1979; Wittenberger, 1981; Rowe, 1996; Dunbar & Barrett, 2000). There are 4 recognised subspecies which can be discriminated through mitochondrial DNA analysis (Morin *et al.*, 1992).

In nature, they have a wide discontinuous distribution throughout central and western equatorial Africa (Vigilant, 2004), occupying a variety of habitats, including woodland savanna, grassland and tropical rainforests (Wallace, 1979; Rowe, 1996), up to 3000m in altitude with home ranges between 3900-7800ha (Rowe, 1996).

Chimpanzees are highly susceptible to human diseases (Cowlishaw & Dunbar, 2000) and exhibit a high genetic overlap with humans (Hancocks, 2001; Sakaki *et al.*, 2002). Because of their exploitation for the pharmaceutical industry, the bushmeat trade, ebola virus outbreaks and the effects of habitat loss (Cowlishaw & Dunbar, 2000; Dunbar & Barrett, 2000; Walsh *et al.*, 2003), chimpanzees are classified as endangered (Vigilant, 2004; IUCN, 2011) although some argue for a higher conservation status (Walsh *et al.*, 2003). Free-ranging population estimates in 2004 were as low as 100 000 individuals (Vigilant, 2004).

Behaviour

Chimpanzees are diurnal (Dunbar & Barrett, 2000) and sleep in arboreal nests, constructed from branches at night (Wallace, 1979). Chimpanzees are both arboreal and terrestrial (Rowe, 1996; Dunbar & Barrett, 2000; Kosheleff & Anderson, 2009) and locomotion is through quadrupedal knuckle walking, bipedal walking, climbing and limited brachiation (Rowe, 1996). 80% of their activity is devoted to foraging (Tweheyo *et al.*, 2004).

Chimpanzees have a catholic diet (approximately 250 food types; Rowe, 1996), comprising fruit (up to 76% of their diet; particularly figs; Rowe, 1996; Cowlishaw & Dunbar, 2000; Dunbar & Barrett, 2000; Tweheyo *et al.*, 2004), leaves (up to 45%), flowers (up to 18%), seeds (up to 11%) and animal material (up to 5%) (Rowe, 1996). Trees are their primary food source (Tweheyo *et al.*, 2004) and concomitantly they are important seed dispersal agents (Cowlishaw & Dunbar, 2000; Dunbar & Barrett, 2000; Tweheyo *et al.*, 2004). Chimpanzee foraging behaviour is highly flexible and chimpanzees occasionally raid crops (Cowlishaw & Dunbar, 2000). Foraging may be performed solitarily but chimpanzees tend to remain in close-knit subgroups (Wallace, 1979) of between three and 11 familiar individuals (Wallace, 1979; Dunbar & Barrett, 2000). Tools are readily manufactured by reintroduced (Farmer et al., 2006) and free-ranging populations for foraging (Rowe, 1996; Morimura, 2003), defence (Wittenberger, 1981) and hunting (Pruetz & Bertolani, 2007). Chimpanzees are skilled hunters (Vigilant, 2004), showing preference for red colobus monkeys *Procolobus badius* (Wittenberger, 1981; Cowlishaw & Dunbar, 2000; Dunbar & Barrett, 2000) and also consuming various small mammal species (Wallace, 1979; Dunbar & Barrett, 2000).

Chimpanzee societies comprise a core group of males and peripheral, nomadic females (Wittenberger, 1981; Rowe, 1996; Cowlishaw & Dunbar, 2000). Females generally leave their natal group around adolescence (Vigilant, 2004), approximately between 9 and 12

years of age (Nishida *et al.*, 2003), and are mobile within and between troops (Wittenberger, 1981; Rowe, 1996; Cowlishaw & Dunbar, 2000; Williams *et al.*, 2002). Chimpanzees mate promiscuously (Rowe, 1996) and up to 50% of female's offspring may be sired by males outside of their home group (Cowlishaw & Dunbar, 2000). Distinct sex-specific behaviour patterns are common both in the wild (Bates & Byrne, 2009), and in captivity (Videan & Fritz, 2007) and are mediated by social status (Celli *et al.*, 2003).

Male chimpanzees apparently form coalitions (Rowe, 1996; Cowlishaw & Dunbar, 2000; Williams *et al.*, 2002) in response to female emigration and the resulting high male densities (Cowlishaw & Dunbar, 2000; Connor & Whitehead, 2005). Male coalitions aggressively defend a territory by patrolling its borders and actively hunting down intruders (Wallace, 1979; Wittenberger, 1981; Vigilant, 2004; Mitani & Watts, 2005). Bonds are maintained through allo-grooming, as it has particular social importance in primates (Henzi *et al.*, 2003), and potentially sharing of meat (Wittenberger, 1981; Rowe, 1996) but more recent work casts doubt on meat functioning as social currency (Gilby, 2006; Gilby *et al.*, 2010; Gomes & Boesch, 2011). Group aggression is rare, typically displaced through grooming, scratching, yawning, rocking back and forth, masturbation, mounting, kissing and hugging (Wallace, 1979). Cooperative behaviour is also uncommon (Hare & Tomasello, 2004) with the exception of defence against predators, such as leopards (Wittenberger, 1981).

Natural chimpanzee populations display culture (Boesch & Tomasello, 1998; Vogel, 1999; Vigilant, 2004), whereby different behaviours are used to achieve the same goal or similar behaviours serve different functions (Boesch & Tomasello, 1998). These cultural patterns of behaviour include tool use, gesturing, food preferences and grooming patterns (Boesch & Tomasello, 1998; Vogel, 1999).

Intelligence and cognition

Social complexity is thought to drive the evolution of intelligence (Kummer & Goodall, 1985) and this is apparent in the chimpanzee. Chimpanzees are capable of complex learning and imitation (Bjorklund & Bering, 2003) which is facilitated through social group interactions (Boesch et al., 1998) as well as, some would argue, teaching (Caro & Hauser, 1992). Chimpanzees are highly intelligent and capable of understanding complex scenarios, such as single invisible displacement (a subject must identify the position of an object placed under one of several occluders, such as cups, which have been swapped in a random fashion: Collier-Baker *et al.*, 2006) and symbolic representation (Dunbar & Barrett, 2000) to the point of being able to communicate via sign language (Rowe, 1996).

Chimpanzees are self-aware (de Veer et al., 2003), experiencing seemingly parallel emotions to humans (King & Landau, 2003) including empathy (Povinelli et al., 1992). Chimpanzees exhibit self-restraint, using self-distraction to control impulsivity (Evans & Beran, 2007). They exhibit distinct personalities (Pederson et al., 2005) and perceive the world in a similar way to humans, from the basic recognition of colours (Matsuno et al., 2004) to the more complex understanding of the actions and intentions of conspecifics and humans.

The social cognition of chimpanzees is relatively well understood through extensive laboratory-based experimentation, and evidence from free-ranging populations suggests that chimpanzees utilize complex socio-cognitive skills under natural conditions as well (Crockford *et al.*, 2012). Chimpanzees understand behavioural goals of individuals (Hassin et al., 2005), including humans, and adjust behaviour accordingly (Povinelli et al., 2003). Chimpanzees understand and manipulate the psychological states of others (Hare & Tomasello, 2004) through inference (MacLean & Hare, 2012), distraction (Hare et al., 2000) and deception of conspecifics (Hirata & Matsuzawa, 2001) and humans (Hare et al., 2006).

Influences of the captive environment on chimpanzees

Given the natural habitat chimpanzees live in, the complexity of chimpanzee sociality and chimpanzee intelligence, many aspects of their captive maintenance are assumed or overlooked completely. My study is not an exhaustive examination of the environmental influences on the behaviour of captive chimpanzees. Rather my study aims to explore some of the overlooked aspects of chimpanzee maintenance as a means of highlighting the necessity to consider all aspects, however subtle or complex, of captive chimpanzee husbandry. Generally, apes are considered to be relatively easy to house in captivity (Hancocks, 2001), largely because primates possess inherent behavioural flexibility (Olsson & Westlund, 2007). The effects of spatial restriction and the associated stress on chimpanzees have been well studied (one of the first investigations into spatial change effects on captive animals was conducted with chimpanzee subjects: Nieuwenhuijsen & de Waal, 1982), but the possibility of chimpanzees utilizing non-social coping strategies in response to spatial change has received scant attention. Chapter 2 of my thesis explores both the non-social and social responses of captive chimpanzees to long-term spatial restriction conditions associated with a change of enclosure, which took place from April 2004 to February 2005.

Associated with enclosure changes, most studies have examined the behaviour of animals immediately following release into new enclosures, with almost no investigations

examining the long-term effects on behaviour. Natural history and ancestry are thought to play a role in determining behaviour (Chang *et al.*, 1999) and many behaviours are believed to reflect potential 'behavioural scars' related to past experience (Swaisgood & Shepherdson, 2005). Despite this, no studies to date have considered the influence of past experience and stress on space use and animal spacing patterns. These themes are explored in Chapter 3; relating a previous spatial environment to the space use and spacing patterns of captive chimpanzees several years after a change in enclosure. The study described in Chapter 3 took place from March to July 2009.

Social enrichment in captive primates has received little attention, largely due to the inherent risks and constant monitoring required (Visalberghi & Anderson, 1993). Nonetheless, social manipulations are commonplace in captivity (Visalberghi & Anderson, 1993) and may be a source of stress to captive animals (Morgan & Tromborg, 2007) but the role of species-typical social changes has not been explored in captivity. The fission-fusion nature of chimpanzee society (Rowe, 1996; Dunbar & Barrett, 2000) lends itself to such investigation and Chapter 4 examines the effects of two species-typical social changes on chimpanzee behaviour. The first, a merging of two groups following a period of separation, took place from February to May 2008 and the second, the removal of an adult female, took place from July to November 2008.

Little information exists on the impact of the thermal environment on primate behaviour (Dahl & Smith, 1985). Zoos typically provide unrealistic thermal environments for primates (Lindburg, 1998) as most primates naturally inhabit tropical climes but are housed at higher latitudes (Coe, 1989). Previous work has suggested that shade may be an important factor in captive ape thermoregulation (Stoinski *et al.*, 2001) and Chapter 5 explores shade as a thermal resource for captive chimpanzees during the austral winter/spring (May – September) period of 2008.

Arrangement of the thesis

This thesis consists of an introductory chapter (Chapter 1), four experimental chapters investigating the themes described above (Chapters 2-5) and a discussion and conclusion chapter (Chapter 6). A seventh appendix chapter describes a study conducted concurrently to the other studies described in this thesis and investigates the role of zoo volunteers in data collection. Each of the experimental chapters is written in a manuscript format, intended for publication. A separate reference list accompanies each chapter, and thus there is some

overlap in referencing between chapters. All tables and figures are numbered sequentially per chapter, while page numbers are numbered throughout the thesis.

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Chapter 2. The role of behavioural flexibility and alternative coping strategies in chimpanzee responses to spatial restriction and enclosure change

Abstract

The captive environment is characterised by spatial restriction and crowding. Many animals exhibit heightened aggression in response to crowding or reduced space, which potentially compromises their wellbeing. Primates however appear to possess mechanisms to control aggression under these conditions. These findings have lead to the proposal of three models for animal responses to crowding: the density-intensity model, tension-reduction and conflict-avoidance models. The aim of this study was to investigate whether changes in available space in two groups of captive chimpanzees at the Johannesburg Zoo, South Africa concurred with any of these three models. In addition, a forth model, based on the coping hypothesis of stereotypic behaviour was tested. Behavioural observations of both chimpanzee groups was conducted throughout the redesign and reconstruction of the chimpanzee exhibit, during which time the chimpanzees were subject to varying degrees of spatial restriction. The results indicated that the family group utilized a conflict-avoidance tactic to mediate aggression during indoor spatial crowding evidenced by increased self-directed behaviour and decreased activity and social interaction. Outdoors however, higher socio-positive behaviour suggests the family group utilized a tension-reduction tactic to prevent aggression. The orphan group also appeared to utilize a tension-reduction tactic during indoor spatial crowding because socio-positive behaviour was higher, while inactivity and self-directed behaviours did not change significantly. As with the family group, the orphans appear to have utilized a tension-reduction tactic in smaller outdoor environments as well. In both groups, indoor spatial crowding generated significant increases in abnormal behaviour. Together, these results provide mixed support for the tension-reduction and conflict-avoidance models, while offering no clear evidence for the density-intensity model. The outcomes suggest that the chimpanzees may have utilized abnormal behaviour as an outlet for the stress of spatial restriction. In addition, the provision of increased space does appear to have welfare benefits and promote more natural behavioural patterns.

Introduction

Non-human primates have been studied in a variety of settings, including free-ranging natural populations, semi-natural populations and captive groups (Drickamer, 1973). While the captive environment can never replicate the natural environment (Drickamer, 1973; Clarke *et al.*, 1982a), 'naturalistic' enclosure designs are considered to be beneficial (Maple & Finlay, 1989; Ogden *et al.*, 1990), encouraging natural behaviour, with persistent ameliorative effects (Ross *et al.*, 2011). However, the captive environment by nature influences the behaviour of animals (Drickamer, 1973) including primates (Novak *et al.*, 1992). Behaviour in captive environments may be altered, both quantitatively (e.g. Caine & O'Boyle, 1992) and qualitatively (e.g. Rumbaugh, 1988), by specific environmental elements. Naturalistic captive enclosures must be designed to generate environments that provide both aesthetic and functional features of the natural environment (Little & Sommer, 2002). However, many aspects such as space availability, and the associated costs (Young, 2003), limit the degree to which the captive environment can mirror the natural environment.

Adequate space is considered vital for the maintenance and wellbeing of captive primates (Honess & Marin, 2006b). The spatial density in which animals live can have a large influence on the behaviour and social structures of the animals concerned (Judge & de Waal, 1997). For example, African stripped mice *Rhabdomys pumilio* utilize a flexible social structure, alternating between communal and solitary living strategies depending on population density (Schradin *et al.*, 2010). Similarly, the spatial restrictions and population densities that captive animals experience are likely to influence their behaviour as well. For this reason, adequate space is considered vital for the maintenance and wellbeing of captive primates (Honess & Marin, 2006b).

Free-ranging primate populations often experience environmental instability and associated changes in aggression levels within groups (Clarke & Mayeaux, 1992). Similarly, changes to the captive environment are likely to elicit changes in aggression due to their effect on social organisation (de Waal, 1989). Aggression appears to be one of the primary drivers of animal spacing, both in nature and captivity (McBride, 1971), but can have deleterious consequences for the animals involved, ranging from altered social status (Raab *et al.*, 1986) to impaired reproduction (Arey & Edwards, 1998). In rats reared under two differing housing conditions, aggression and mortality were greater under burrow conditions than open housing conditions (Blanchard *et al.*, 1985). Père David's deer experienced increased stress and associated aggression in various physical environments and different

social conditions (Li *et al.*, 2007). The management of aggression within animal groups is thus critical to the maintenance of both group cohesion and individual health. Captive animals in particular are frequently subject to extreme conditions of both the social and physical environment (Judge & de Waal, 1993), placing them at risk of the deleterious effects of escalating aggression.

Observations of animal responses to spatial restriction lead to the development of a 'density-intensity' model (*sensu* Nieuwenhuijsen & de Waal, 1982), whereby reductions in available space lead to increased social stress and escalating aggression. Studies such as that of Calhoun (1962) exemplified this idea and evidence suggests that individuals under crowding experience heightened social stress (Aureli & de Waal, 1997; Cordoni & Palagi, 2007; Tacconi & Palagi, 2009). Subsequently, a number of other studies have provided support for this model. Animals are thought to experience elevated levels of stress when housed under crowded conditions (Li *et al.*, 2007; Morgan & Tromborg, 2007) and the spatial-density model was also supported by a number of studies in the agricultural setting (e.g. Blanc & Thériez, 1998; Blanc *et al.*, 1999). Studies of captive chimpanzees (Ross *et al.*, 2010), captive bonobos *Pan paniscus* (Sannen *et al.*, 2004), stumptailed macaques *Macaca arctoides* (Demaria & Thierry, 1989), pigtail macaques *Macaca nemestrina* (Erwin & Erwin, 1976) and galagos *Galago senegalensis braccatus* (Nash & Chilton, 1986) all reported higher levels of aggression in comparatively small environments. These results suggested that the relationship between space and aggression was clear-cut.

Yet, some studies found mixed support for the density-intensity model. When housed in their small indoor enclosure and their larger outdoor enclosure, captive chimpanzees *Pan troglodytes* displayed higher levels of aggression indoors, but the aggression was low in relation to the differences in size between the two enclosures (Nieuwenhuijsen & de Waal, 1982). A similar study of pigtail macaques found that levels of aggression increased with increasing density, but that there was evidence that it was socially regulated (Anderson *et al.*, 1977). Subsequently, de Waal (1989) suggested that the relationship between space and aggression was not as simple as assumed. He argued that primates place a great deal of value in their social relationships and may modify their social interactions to counteract increased aggression risk (de Waal, 1989). Primates are known to have a number of mechanisms, such as reconciliation and appeasement behaviours, to limit the expression of aggression in social groups (Judge *et al.*, 2006). de Waal's 'coping model' suggested that primates might selectively employ these mechanisms to manage aggression (de Waal, 1989).

The coping model received support in subsequent investigations. Support stems from studies of macaques (Stumptailed macaques *Macaca arctoides*: Demaria & Thierry, 1989; Rhesus macaques *Macaca mulatta*: Novak *et al.*, 1992), green monkeys *Cercopithicus aethiops* (Clarke & Mayeaux, 1992), hamadryas baboons *Papio hamadryas hamadryas* (Judge *et al.*, 2006), gorillas *Gorilla gorilla gorilla* (Cordoni & Palagi, 2007) and bonobos (Sannen *et al.*, 2004). However, as with the density-intensity model, many studies found results suggesting an alternative to this coping strategy.

A number of studies found that primates appear to avoid conflict altogether by minimizing their social interactions, an alternative to the social buffering effect of the coping model. Rhesus macaques increased their avoidance of conspecifics and reduced their intense aggression, favouring milder forms of aggression (Judge & de Waal, 1993) while long-tailed macaques *Macaca fascicularis* reduced activity levels and only increased levels of mild aggression (Aureli *et al.*, 1995) under short-term crowding. Similarly, chimpanzees reduced activity levels and social contact under spatial crowding (Aureli & de Waal, 1997) and olive baboons *Papio anubis* increased agonistic behaviour but reduced activity under artificial crowding conditions (Elton & Anderson, 1977).

Based on the findings of the primate spatial restriction studies, two possible coping strategies were suggested as constituents of the coping model: the tension-reduction and conflict-avoidance strategies (Videan & Fritz, 2007). Many studies have found mixed support for these strategies. Rhesus macaques engaged in avoidance behaviour, suggesting a conflict-avoidance strategy, but also increased huddling under crowding, suggestion tension-reduction (Judge & de Waal, 1993). Gorillas increased reconciliation behaviour, suggesting a tension-reduction strategy, but also increased avoidance and inter-individual distances in their smaller indoor enclosures relative to their larger outdoor enclosures, in line with a conflict-avoidance strategy (Cordoni & Palagi, 2007). Male rhesus macaques conformed to the tension-reduction strategy, whereas females appeared to display aggression as a function of social density as predicted by the density-intensity model (Judge & de Waal, 1997).

Judge & de Waal (1997) also suggested that the strategy utilized by the group may be dependent on the length of time that the individuals are exposed to spatial crowding. Short-term crowding, usually considered to be anything from 20 minutes (Anderson *et al.*, 1977) to a number of hours (Judge & de Waal, 1993; Aureli *et al.*, 1995), appears to generate conflict-avoidance. Longer crowding periods, ranging from a number of months (Nieuwenhuijsen & de Waal, 1982) to several years (Judge & de Waal, 1997), instead elicit tension-reduction behaviour as the animals are afforded more time to adjust to their environmental conditions

(Nieuwenhuijsen & de Waal, 1982). However, primates are behaviourally plastic and may well engage in several strategies in response to spatial crowding (Judge & de Waal, 1993).

The lack of aggression displayed by many primates under crowding conditions does not necessarily mean that they are not stressed (de Waal, 1989). Nieuwenhuijsen & de Waal (1982) reported increased faeces manipulation and hair plucking during winter crowding periods, behaviour associated with increased stress (Reinhardt, 2005). Hamadryas baboons increased displacement activities (Judge *et al.*, 2006), gorillas increased self-directed scratching behaviour (Cordoni & Palagi, 2007) which is a reliable measure of anxiety in primates (Maestripieri *et al.*, 1992), rhesus macaques exhibited self-injurious behaviour (Judge & de Waal, 1993), another behaviour associated with increased stress (Reinhardt & Rossell, 2001), and juvenile olive baboons increased self-injurious behaviour and hair-plucking and ingestion (Elton & Anderson, 1977) under crowding. Even Calhoun's study of rats found elevated levels of abnormal behaviour and social pathology, including cannibalism, in crowded populations (Calhoun, 1962).

The function of abnormal behaviours remains somewhat unclear. Many appear to be strongly related to stress alleviation (e.g. regurgitation/re-ingestion: Baker & Easley, 1996; self-injurious behaviour: Tiefenbacher *et al.*, 2004) and may be responses to the restricting captive environment (Walsh *et al.*, 1982). This idea was formalized in the 'coping hypothesis', originally coined by Rushen (1993), which suggests that abnormal behaviours may serve a coping role, by reducing the experienced stress of an individual.

Both the coping model, *sensu* de Waal (1989), and the coping hypothesis, *sensu* Rushen (1993) provide a framework of strategies for coping with stress but the mechanisms of each differ considerably (existing social mechanisms in the coping model : de Waal, 1989; non-social mechanisms in the coping hypothesis: Rushen, 1993). In addition, abnormal and self-directed behaviours may offer primates an outlet which minimizes the risk of disrupting the established social relationships, considered to be critical to primate social functioning (de Waal, 1989). Yet, no studies of the crowding effect on primates have considered non-social abnormal behaviours (with the exception of one study where the displacement activities noted included pacing and self-scratching, but did not explicitly examine abnormal behaviour; Judge *et al.*, 2006) as a possible outlet for the social stress experienced under crowding.

The aim of this study was to investigate the behavioural responses of two mixed sex groups of captive chimpanzees to long-term spatial restriction associated with the reconstruction of their outdoor enclosures at the Johannesburg Zoo, South Africa, in relation to the 'density-intensity', 'tension-reduction' and 'conflict-avoidance' models. If the 'density-

intensity' model is supported and the chimpanzees appear to have no intrinsic means of regulating aggression, aggression should escalate under crowding. Little or no increase in aggression would suggest that either the 'tension-reduction' model is supported (associated with increased socio-positive interactions) or the 'conflict-avoidance' model is supported (associated with decreased socio-positive interactions and increased non-social behaviour). Alternatively, but not mutually exclusive of the 'tension-reduction' and 'conflict-avoidance' models, the chimpanzees may increase abnormal behaviour during crowding as an outlet for the social stress of spatial crowding.

Materials and Methods

Study subjects and housing throughout the study

The study was carried out at the Johannesburg Zoo from April 2004 to February 2005. The study subjects included two groups of socially housed chimpanzees. The one group (referred to as the family group) comprised a family unit consisting of two males (Thabu: 21 years; Amber: 5 years) and three females (Daisy: 20 years; Zoe: 9 years; Joyce: 1 year). The second group (referred to as the orphan group) comprised five chimpanzees rescued by the Jane Goodall Institute South Africa and one resident zoo male temporarily housed together. The group included four males (Yoda: 12 years, the resident male; Abu, Amadeus: both 7 years; Niki: 5 years) and two females (Claudette, Lilly: both 7 years). Both groups were housed separately.

During this study, the groups were housed in three different settings. The initial enclosures (old enclosures) and final enclosures (new enclosures) were at the same location (The Johannesburg Zoo Ape House, hereafter referred to as the ape house). However, when the new enclosures were being built - over the old enclosures - the orphan group was housed temporarily at the zoo’s veterinary hospital while the family group was housed in the existing ape house night rooms of the enclosures that were under construction. Each group was housed in an outdoor enclosure during the day and an indoor room (night room) at night at all stages of the experiment, except for the family group which had no access to an outdoor enclosure during the construction period.

Housing prior to reconstruction

Both chimpanzee groups were housed in the old enclosures at the ape house for approximately 13 weeks from the start of observations to the beginning of the reconstruction. The initial outdoor enclosures at the ape house had an area of approximately 100m^2 each and were surrounded by a continuous 4m wide moat of water, with a 30cm high, electrified fence running the full length of the moat midway across it (Figure 1). At the centre of the enclosure was a 72m^2 patch of grass and soil, surrounded by a 1.5m wide paved area, which included several large rocks and two dead tree stumps, with a large 3m high wooden climbing apparatus. All other surfaces were face brick or tiled. Two entrances to the night rooms were set into the back walls of the enclosure in the family enclosure whereas the orphan enclosure had only one entrance. The rear walls also contained three concrete climbing platforms (approximately 0.5m x 0.3 m) set into them. The public were able to observe the chimpanzees from across the two moats, opposite the rear walls of the enclosure.

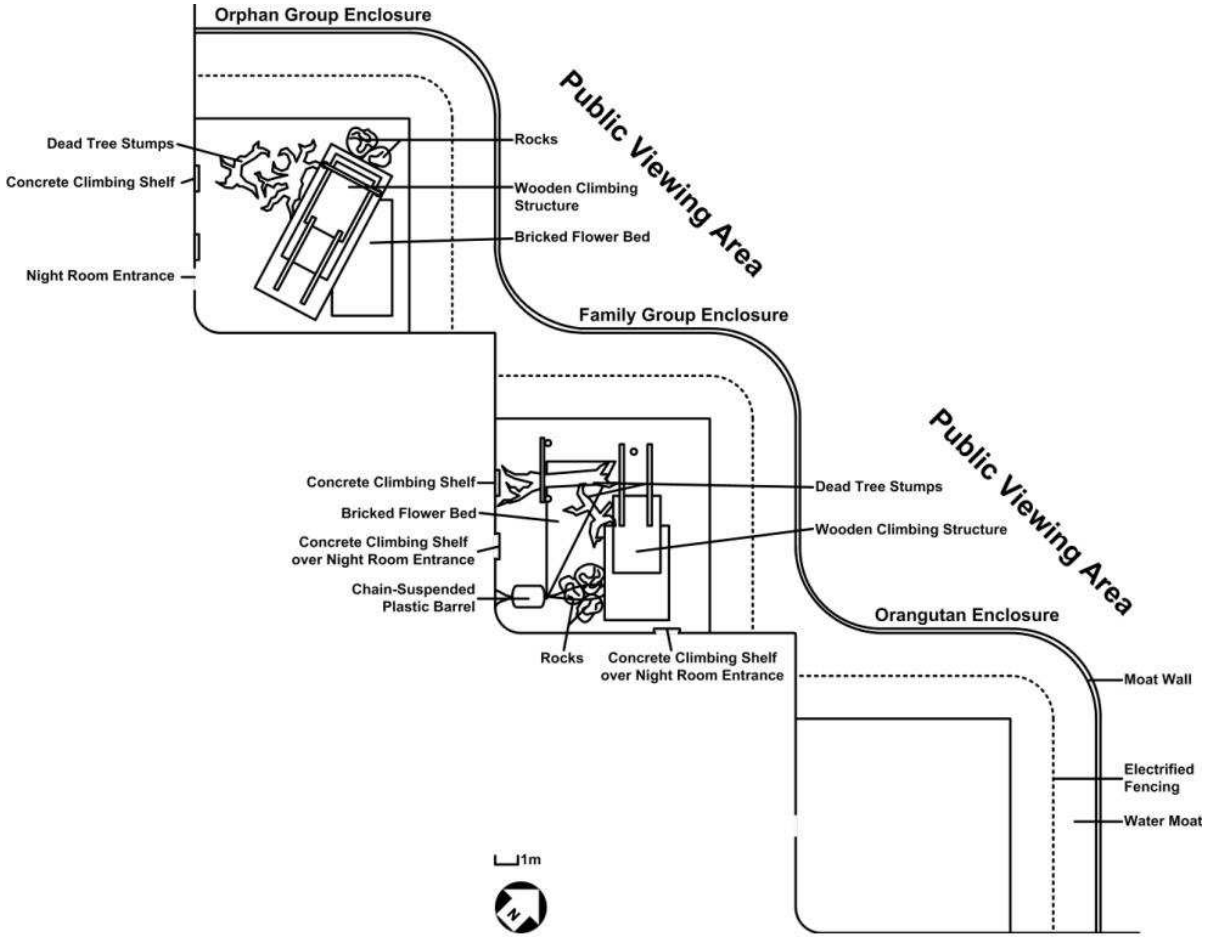

Figure 1. The old outdoor enclosures of the Johannesburg Zoo Ape House, South Africa, drawn to scale

Housing during reconstruction

The family group were housed in the four night rooms at the ape house, each of varying size and complexity (Figure 2). Because construction took place in the adjacent outdoor enclosures, the family group was frequently moved between night rooms. They were observed under these conditions for approximately seven weeks.

The four night rooms all had a similar design, consisting of an open floor area (ranging between 26m^2 and 43m^2), a concrete and rock 'cliff-shelf' (approximately 2.7m tall) which created an elevated floor area that ranged between 8m^2 and 20m^2 and a large reinforced glass viewing window on at least one side of the room. Two of the night rooms had metal climbing structures built into them and the other pair of rooms was connected by a small, lockable gateway. All rooms had a 1.5m long tunnel (approximately 1m high) which linked the night room to the adjacent outdoor enclosure as well as a small alcove built into the 'cliff-shelf' with a barred window, looking out into the keeper access passage (a 1m wide passage running behind all the night rooms from which keepers and animal attendants were able to access the rooms).

The indoor enclosures (Figure 3) of the veterinary hospital, where the orphan group was housed during construction, were approximately 8.5m^2 and were connected to the corresponding outdoor enclosure of approximately 4.2m^2. In order to accommodate the orphan group, the chimpanzees were given free reign of three such adjacent enclosures, the three enclosures being connected by small doorways in the dividing walls of the outdoor sections. The enclosures contained a few tree stumps and branches for climbing and, at one point, the chimps were provided with car tires as enrichment. The orphan group were also observed, under these conditions, for approximately 7 weeks.

Housing following completion of the reconstruction

Once the new enclosures were complete, all the chimpanzees were moved back to the ape house. The new enclosures comprised three 'islands' (Figure 4). The first island was constructed in place of the old orangutan enclosure, the second in place of the old family enclosure and the third in place of the old orphan enclosure (see Figure 1). Each island varied in size and housed a separate group of animals; the first island (±1000m^2) housed the family group, the second (±1500m^2) housed the orphan group and the third housed the orangutans. Both chimpanzee groups were observed for approximately eight weeks in their new enclosures.

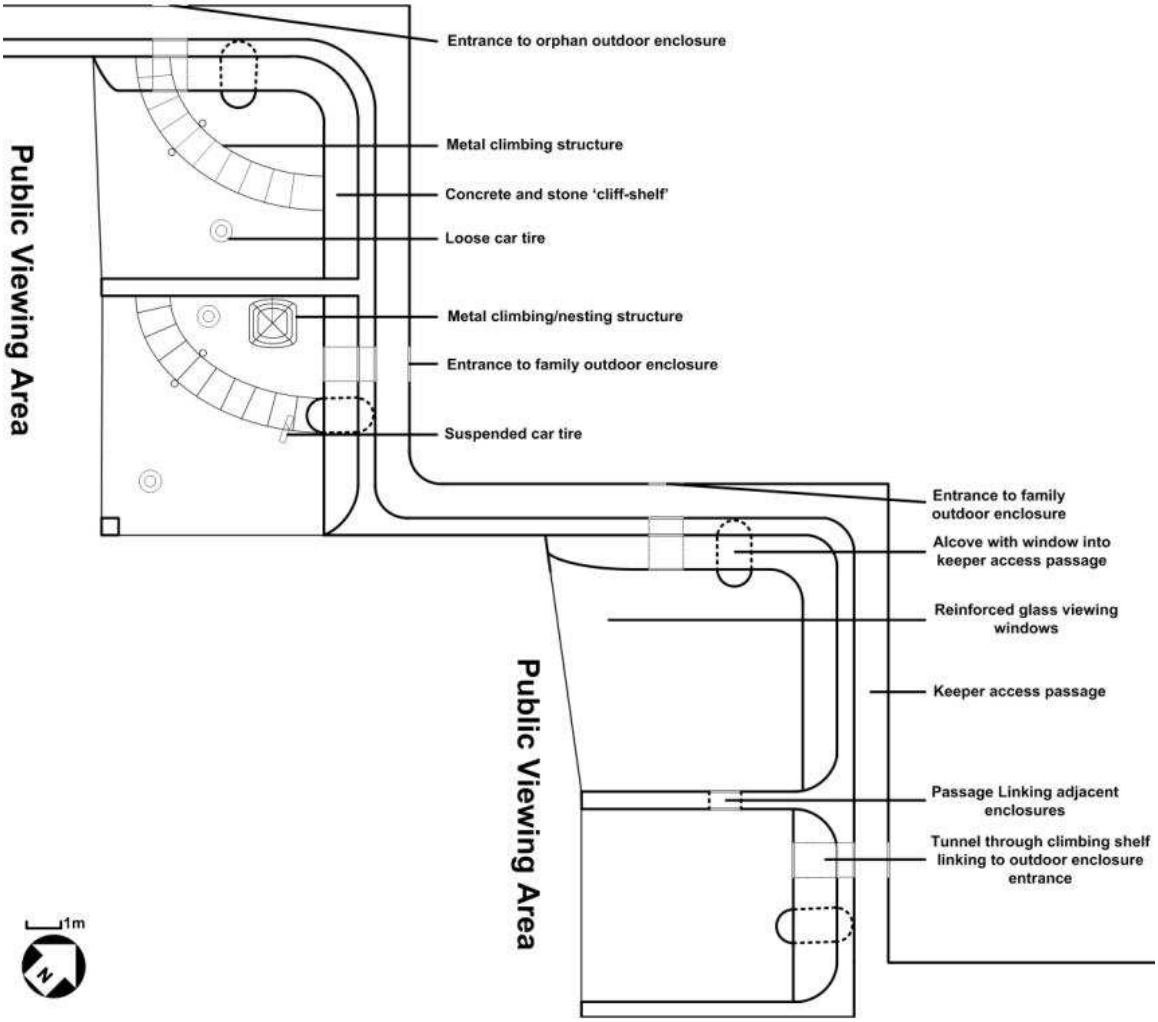

Figure 2. The night rooms of the Johannesburg Zoo Ape house, South Africa, where the family group were housed during the reconstruction of the chimpanzee exhibit, drawn to scale

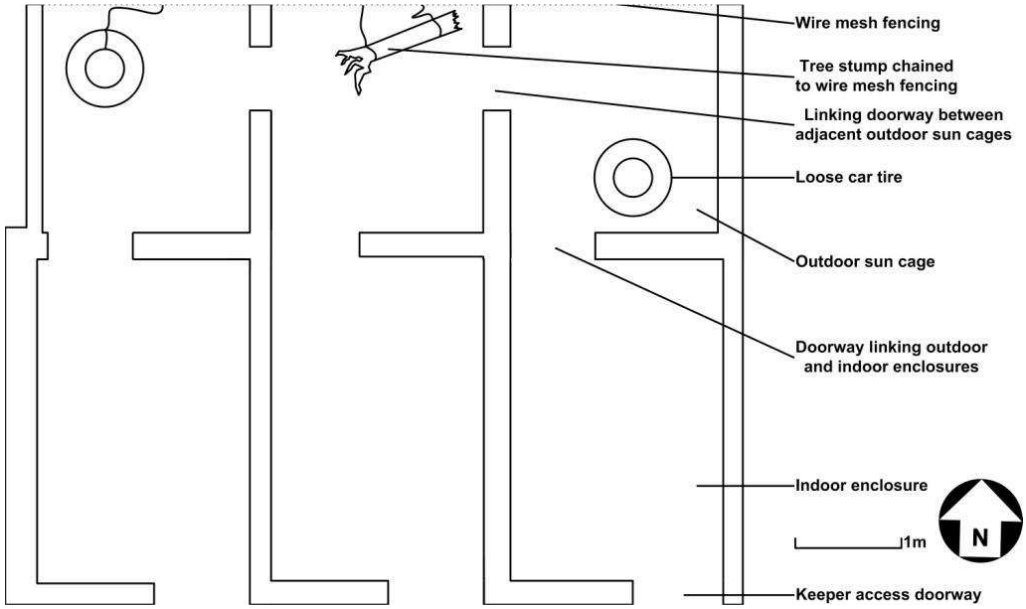

Figure 3. The indoor and outdoor enclosures of the veterinary hospital at the Johannesburg Zoo, South Africa, in which the orphan group was housed during the reconstruction of the chimpanzee exhibit, drawn to scale

Novelty has been highlighted as a possible confound of many crowding studies (Nash & Chilton, 1986; Marriott & Meyers, 2005). Galagos were found to be significantly affected by novelty, an effect which interacted with spatial crowding as well (Nash & Chilton, 1986). For this reason, follow-up observations of the chimpanzee groups in their new enclosure were then carried out 10 weeks later, for five weeks.

All new enclosures were surrounded, on most sides, by 8m high walls, capped with electrified fencing, with entrances to the night rooms in the rear walls. All other sides were surrounded by 4-5m wide moats with 1m high electrified fencing along the edge of the moat and 30cm high fencing 2m into the moat. The moat surrounding the first island had a small indentation to facilitate the chimpanzees' access to water. A stream linked the upper and lower moats surrounding the second island, also permitting the chimpanzees to access water.

Large trees, other vegetation, several large rocks and fallen logs were located in both the first and second islands. The second island also had a rock outcrop. Trees that exceeded 6m in height and those that extended over the moat to the public viewing areas had electrified fencing around the circumference of the trunk to prevent escapes.

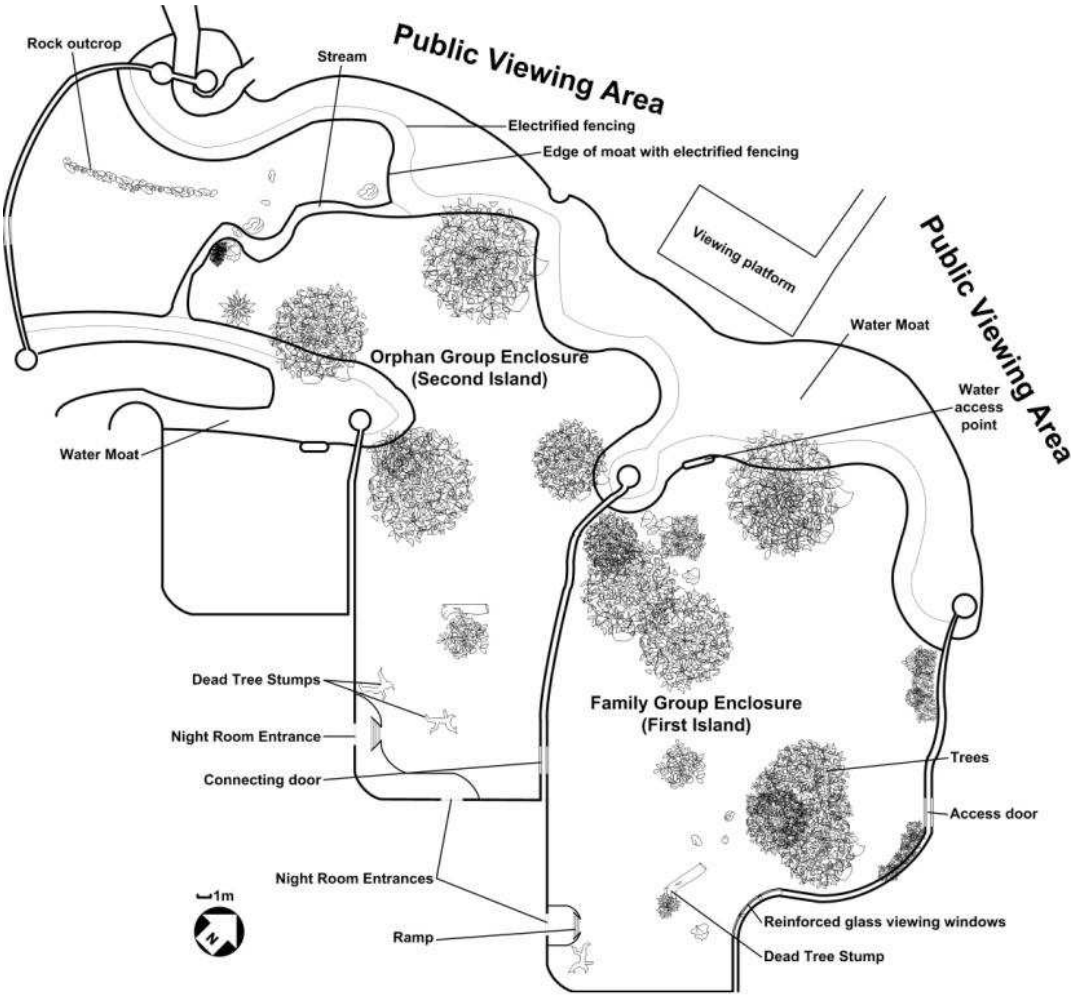

Figure 4. The new outdoor enclosures of the Johannesburg Zoo Ape House, South Africa, drawn to scale

Husbandry

Under all the housing conditions, the chimpanzees were fed and maintained according to a similar schedule. They were given a variety of fresh fruit and vegetables, primate pellets and occasionally boiled eggs twice daily, at approximately 09h00 in their outdoor enclosure as an incentive to leave the night room, and again at 15h00 on weekdays (16h00 on weekends) in their night rooms to encourage them to return into the indoor night rooms. During periods when the chimpanzees were outside, keepers cleaned the indoor enclosures and straw was provided as nesting material in the night rooms only. On particular days, the chimpanzees were kept in their night rooms throughout the day. This was typically due to problems with the electric fencing in the outdoor enclosures, or necessitated by veterinary procedures. During construction, when the family group were housed indoors, they were moved between night rooms for cleaning and feeding.

Behavioural observation

Behaviour of the chimpanzees was observed and recorded prior to, throughout and immediately after the reconstruction in both the indoor and outdoor environments wherever possible. Approximately two months after the release of the chimpanzees into the new enclosures, follow-up observations were conducted. Under all housing conditions, behaviour was recorded using the instantaneous scan sampling method (Martin & Bateson, 1986), with a sample interval of 30 seconds for all individuals in the group. Sampling sessions were conducted between one and five times a week, lasting 30 minutes each. Sessions were conducted at varying times between 09h00 and 11h00, and between 12h00 and 14h30. Behaviour was recorded according to the categories listed in Table 1.

Data analysis

The data were classified according to the group observed (family or orphan), location (indoors or outdoors) and treatment (baseline, reconstruction, new enclosure and follow-up). In order to determine which behaviours to use in further analyses, a factor analysis was used for the combined groups' data for the indoor and outdoor enclosures respectively. Based on the outcome of the factor analysis for the indoor enclosures I used all the behaviours observed in further analysis with the exception of the categories for public interaction and hidden. The chimpanzees' limited opportunities to interact with the public in their night rooms resulted in very low levels of interaction (less than 0.9% of recorded behaviour). In addition, the enclosures themselves offered no cover so there is little possibility for the

animals to hide. For the outdoor enclosures, all factors except public interaction were included in further analyses. While this environment offered more opportunities for interactions, the animals did not interact with the public often (less than 0.8% of recorded behaviour).

Table 1. Definitions of behaviours observed in the chimpanzee groups at the Johannesburg Zoo, South Africa, during the reconstruction of the chimpanzee exhibit

Behaviour	***Definition***
Manipulate non-edible items	Manipulation of and interaction with non-edible objects or items (e.g. object play with a non-edible object such as a rock and tool use)
Manipulate edible items	Manipulation of and interaction with edible items (e.g. foraging and object play with an edible object such as a fruit)
Inactive	Lack of activity. Included lying down, sitting and standing idly
Self-directed	Self-grooming, masturbation and non-abnormal body manipulation
Socio-positive	Allogrooming. Social play including wrestling, playful biting and playful chasing (characterised by a relaxed face, possibly with a drooping lower lip, or a full play face. Usually silent but may include soft grunts or hoots; Goodall, 1986)
Socio-negative	Chasing aggressively (characterised by sneering, open and closed grins and compressed lip faces. Usually associated with screams, barks and 'wraaa' calls; Goodall, 1986) or fighting with one another. Included aggressive gesturing or signalling
Travel	Locomotion from one location to another, included tree climbing and locomotor and solitary play
Public interaction	Interaction, positively or negatively, with the public through displays begging and throwing of objects at the public
Abnormal	Behaviour that appeared abnormal in context, such as nipple pulling, abnormal walking, coprophagy, self mutilation, faeces throwing and hair plucking
Hidden	Any time that the chimpanzees were not clearly visible or their behaviour was not discernable

Following this, for all chimpanzee groups, and for all treatments, generalized linear models (GLZ) were used, with appropriate link functions. Generalized linear models are appropriate for binary response variables, such as those in this study, as they do not assume a normal distribution (Crawley, 2007). Behaviour data for the indoor and outdoor enclosures were analysed separately. All analyses were two-tailed and were conducted using Statsoft Statistica 8.0 (StatSoft, 2008). Behaviour was coded as counts of the absence and presence of a behaviour because the expression of one behaviour often precludes the expression of another. This coding resulted in a binomial absence/presence count for each behaviour which was used as the response variable in the GLZs while the categorical predictors included treatment (baseline, reconstruction, new enclosure, follow-up) and behaviour (Table 1). Within-factor significant differences were assessed through the use of β-estimates and confidence intervals and were considered as significant for $p \leq 0.05$. First order effects

(treatment; behaviour) were not examined in detail whereas second order effects (treatment*behaviour) were. This was done to more directly address the aims of the study.

Results

A total of 110 hours of data were collected for the family group (61.25 hours indoors, 48.75 hours outdoors) and 93 hours for the orphan group (52.5 hours indoors, 40.5 hours outdoors).

Family group

For the family group in the indoor environment, construction treatment was found to be a significant predictor of behaviour (Wald $\chi^2_2 = 6.990$; $p = 0.030$). Across all treatments, all behaviours were found to be significantly different (Wald $\chi^2_6 = 1227.172$; $p < 0.001$).

A significant indoors treatment*behaviour effect was found as well (Wald $\chi^2_{12} = 245.581$; $p < 0.001$; Figure 5). Object manipulation levels were significantly lower only in the new treatment than the other two treatments. Inactivity was significantly lower in the baseline treatment than other treatments. Self-directed behaviour was significantly lower in the new enclosure treatment than either the baseline or reconstruction treatments. Socio-positive behaviour differed significantly between all treatments but was highest during the baseline and lowest during the new enclosure treatments. Socio-negative behaviour did not differ significantly between the three treatments. Significantly more travelling was recorded during the new enclosure than baseline treatment, which was significantly higher than the reconstruction treatment. Abnormal behaviour was significantly higher during the reconstruction than during either the baseline or new enclosure treatments.

In the outdoor enclosures, the construction treatment was not found to be a significant predictor of the family group's behaviour (Wald $\chi^2_2 = 0.064$; $p = 0.968$). However, within all treatments, all behaviours were found to differ significantly (Wald $\chi^2_7 = 1531.301$; $p < 0.001$). As with the indoor environment, a significant reconstruction treatment*behaviour interaction effect was found (Wald $\chi^2_{14} = 742.609$; $p < 0.001$; Figure 6).

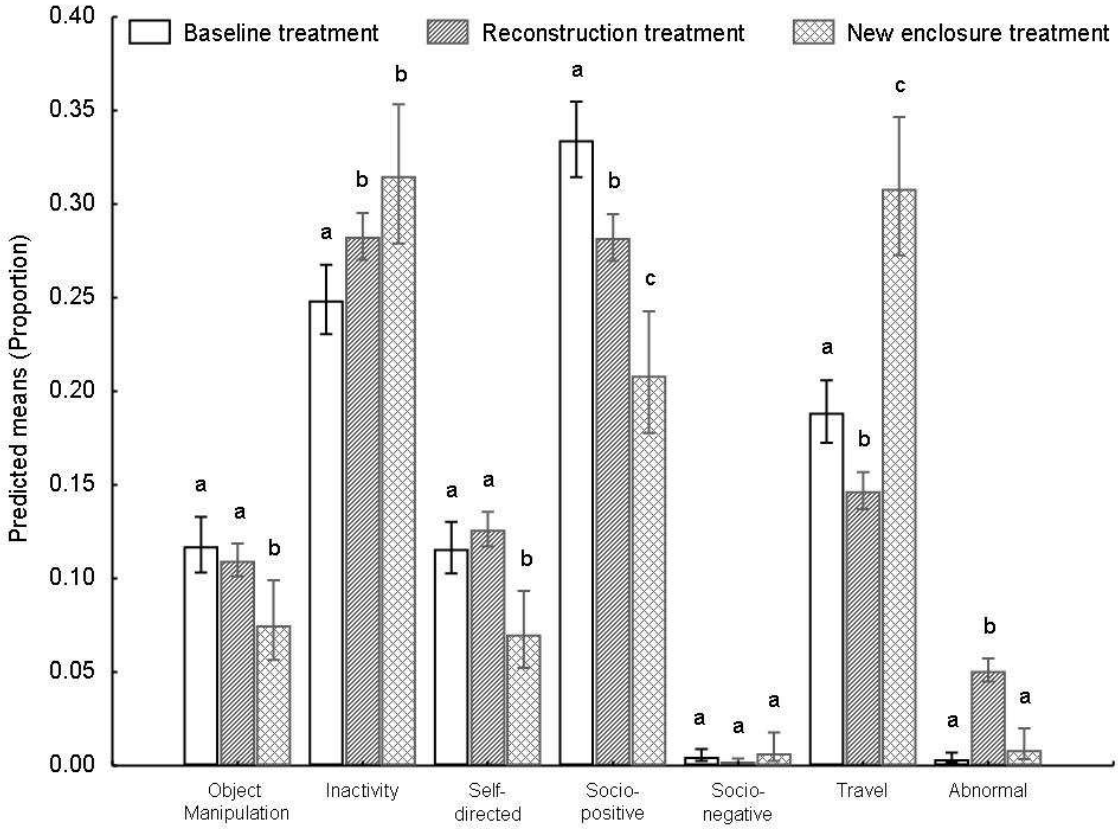

Figure 5. Changes in levels of recorded behaviours across three reconstruction treatments (Baseline, Reconstruction and New enclosure) of the family group at the indoor Johannesburg Zoo chimpanzee exhibit, South Africa. Bars denote predicted mean proportions generated through a generalized linear model for each of the behaviours observed. Whiskers denote 95% confidence limits. Letters above bars denote significant differences between treatments

There was no significant change in the levels of inactivity and socio-negative behaviour across the three treatments. Object manipulation was significantly higher in the new enclosure than baseline treatment, and significantly higher still in the follow-up treatment. Self-directed behaviour was lowest during the follow-up treatment and highest during the baseline treatment but differed significantly across all three treatments. Socio-positive behaviour was significantly higher during the baseline treatment and significantly lower during the follow-up treatment than during the new enclosure treatment. Travel was significantly more prevalent in the new enclosure and follow-up treatments than baseline levels. Abnormal behaviour was significantly higher during the baseline and new enclosure treatments than the follow-up treatment. The chimpanzees spent significantly more time hidden from view in the new enclosure treatment then either the baseline or follow-up treatments.

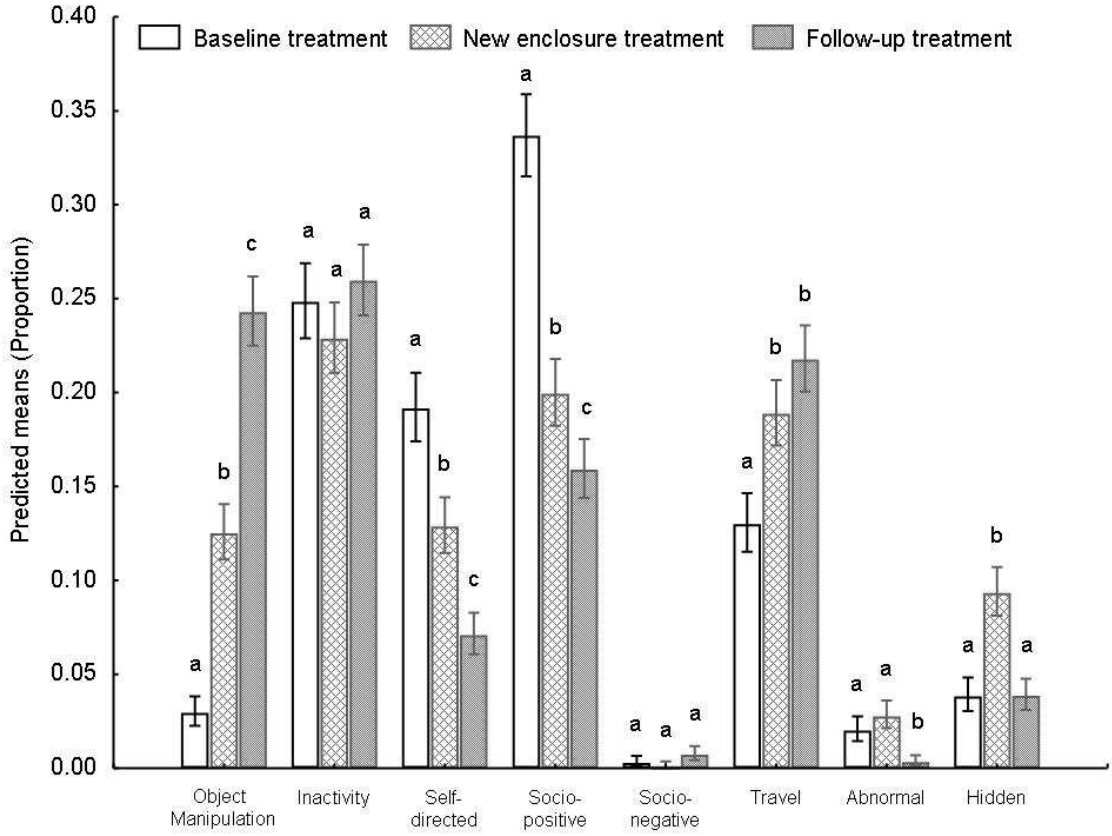

Figure 6. Changes in levels of recorded behaviours across three reconstruction treatments (Baseline, New enclosure and Follow-up) of the family group at the outdoor Johannesburg Zoo chimpanzee exhibit, South Africa. Bars denote predicted mean proportions generated through a generalized linear model for each of the behaviours observed. Whiskers denote 95% confidence limits. Letters above bars denote significant differences between treatments

Orphan group

For the orphan group in the indoor environments, construction treatment was a significant predictor of behaviour (Wald $\chi^2_2 = 13566.23$; $p < 0.001$) and all behaviours were found to be significantly different from one another (Wald $\chi^2_6 = 554.56$; $p < 0.001$). A treatment*behaviour interaction was also found to be significant (Wald $\chi^2_{11} = 204.91$; $p < 0.001$; Figure 7).

Object interaction was significantly higher during the baseline treatment than the reconstruction and new enclosure treatments. Inactivity did not change significantly across all three treatments. The only significant differences in self-directed behaviour were between the reconstruction and new enclosure treatments where higher levels of self-directed behaviour were seen in the new enclosure treatment. Socio-positive behaviour showed only a significantly lower baseline level than in either the reconstruction or new enclosure treatments. Socio-negative behaviour was significantly lower in the reconstruction treatment than baseline and was not observed in the new enclosure treatment. No significant differences

were found between the baseline and new enclosure treatments in terms of travel behaviour, but levels during the reconstruction treatment were significantly lower than in the other two treatments. Abnormal behaviour was significantly higher in the reconstruction and new enclosure treatments than baseline levels.

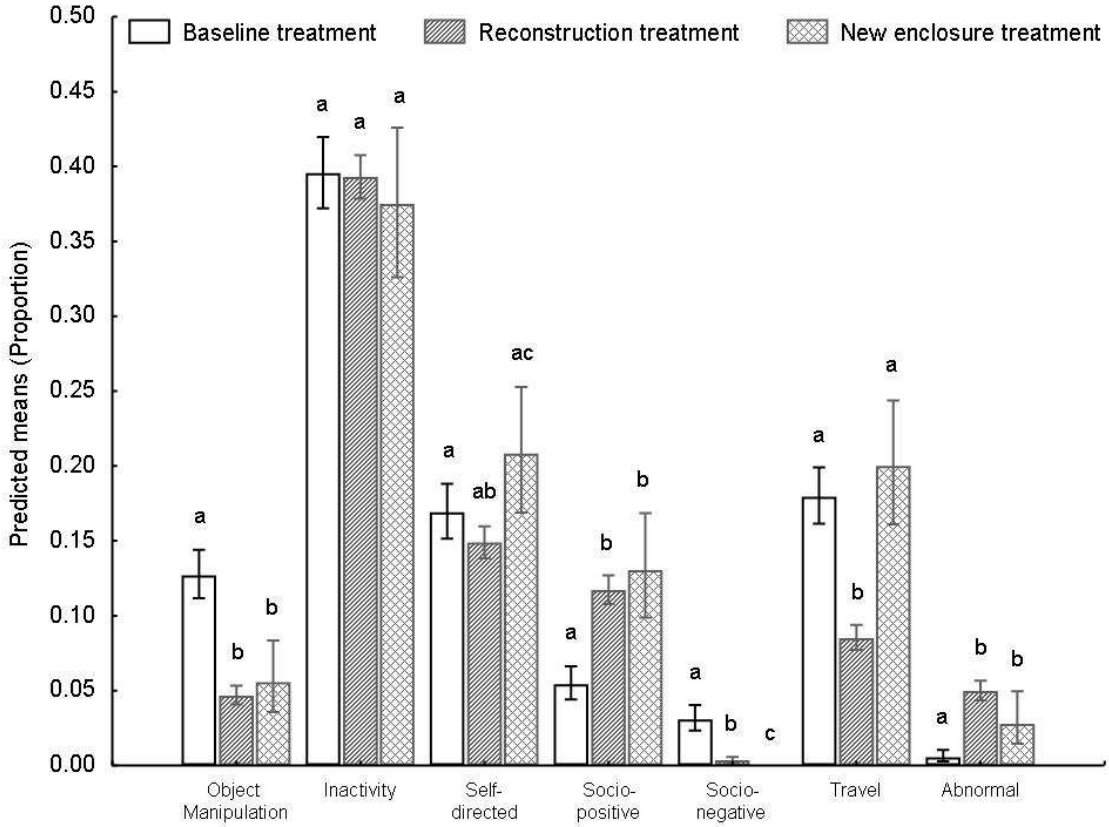

Figure 7. Changes in levels of recorded behaviours across three reconstruction treatments (Baseline, Reconstruction and New enclosure) of the orphan group at the indoor Johannesburg Zoo chimpanzee exhibit, South Africa. Bars denote predicted mean proportions generated through a generalized linear model for each of the behaviours observed. Whiskers denote 95% confidence limits. Letters above bars denote significant differences between treatments

In the outdoor enclosures, a significant treatment effect was found for the orphan group (Wald $\chi^2_2 = 22.774$; $p < 0.001$). All behaviours were found to be significantly different from one another (Wald $\chi^2_7 = 2948.849$; $p < 0.001$) and a significant treatment*behaviour effect was found for the orphan group in the outdoor enclosures (Wald $\chi^2_{14} = 554.060$; $p < 0.001$; Figure 8).

Significant differences in object manipulation were found between the baseline and follow-up treatments, but not between the new enclosure treatment and the other two treatments. Inactivity was significantly lower in the new enclosure treatment than the other two treatments. Self-directed behaviour was significantly lower in the follow-up treatment

than either baseline or new enclosure treatments, which did not differ. Socio-positive behaviour was significantly different across all three treatments and was highest in the baseline treatment and lowest in the follow-up treatment. Both socio-negative behaviour and abnormal behaviour did not differ significantly across all three treatments. Travel was significantly higher during the follow-up treatment than in either the baseline or new enclosure treatments, which did not differ significantly. Significantly more time was spent out of view in the new enclosure and follow-up treatments than baseline levels. Hidden scores were also significantly higher during the new enclosure treatment than the follow-up treatment.

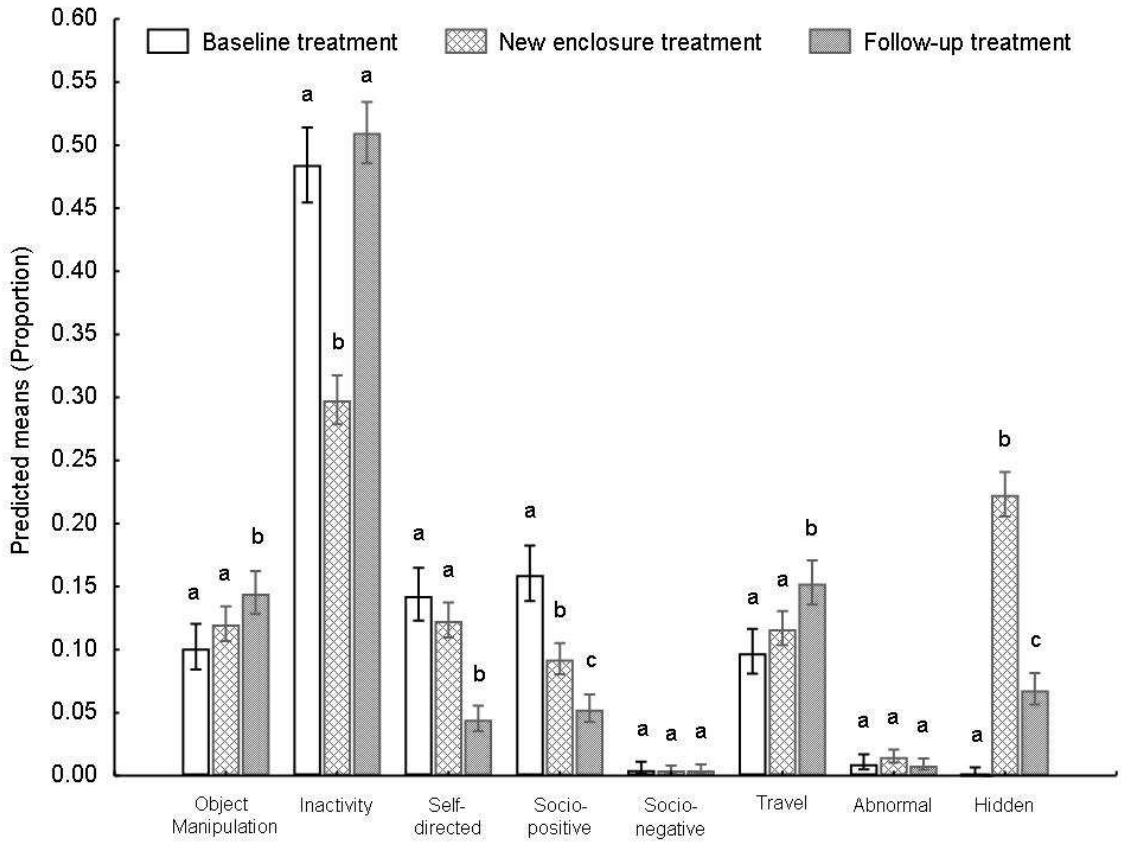

Figure 8. Changes in levels of recorded behaviours across three reconstruction treatments (Baseline, New enclosure and Follow-up) of the orphan group at the outdoor Johannesburg Zoo chimpanzee exhibit, South Africa. Bars denote predicted mean proportions generated through a generalized linear model for each of the behaviours observed. Whiskers denote 95% confidence limits. Letters above bars denote significant differences between treatments

Discussion

The aim of this study was to examine the responses of two chimpanzee groups to long-term spatial restriction as the result of the reconstruction of their enclosures and relate the observed responses to the existing models of coping with spatial restriction in the literature. The results of my study provide mixed support for both the 'tension-reduction' and 'conflict-avoidance' models proposed as part of de Waal's (1989) coping model, but no evidence for the 'density-intensity' model.

The tension-reduction model suggests that primates engage in positive social interactions as a means of placating others and thereby preventing aggressive outbursts (de Waal, 1989). Were this the case, relatively small environments should lead to higher levels of socio-positive interactions when compared to larger environments. In my study, the responses of both chimpanzee groups to spatial change in the outdoor enclosures provide some support for this idea. Both groups displayed significantly higher levels of socio-positive behaviour in their old, smaller outdoor enclosures than in the new, larger enclosures. Enclosure novelty can influence primate behaviour (Nash & Chilton, 1986) and the novelty effect of the larger outdoor enclosures was clearly evident in this study. For both the orphan and family groups, behaviours that differed between treatments showed a significant change between the new enclosure and follow-up outdoor treatments. This is unsurprising as both the qualitative and quantitative changes in the outdoor housing was substantial. Novelty aside, both groups appear to conform to the tension-reduction model when considering the outdoor enclosures.

The responses of the orphan group in the indoor enclosures also appear to support the tension-reduction model as the orphans exhibited lower socio-negative behaviour and higher socio-positive behaviour during the indoor reconstruction treatment, when compared to the baseline treatment. However, when examining the overall levels of social and non-social behaviours, it is clear that the orphan group consistently exhibited low levels of social behaviour, suggesting that a conflict-avoidance strategy may be more likely. The conflict-avoidance model suggests that individuals may prevent aggression by avoiding social interaction completely, favouring non-social behaviours (Videan & Fritz, 2007). In the case of the orphans, the lack of significant changes in inactivity and self-directed behaviour during reconstruction do not support the conflict-avoidance model, suggesting that while levels of socio-positive behaviour were low, the chimpanzees still utilized a tension-reduction strategy. In contrast, the behaviour of the family group seems to conform to a conflict-avoidance strategy, evidenced by no change in socio-negative behaviour, more abnormal behaviour and

inactivity and lower socio-positive, travel and object manipulation behaviour during the indoor reconstruction treatment compared to baseline. Self-directed behaviour was also significantly lower during the indoor new enclosure treatment, which conforms to the expected outcomes of the conflict-avoidance model.

The family group also displayed higher levels of inactivity and lower socio-positive and object manipulation in the indoor new enclosure treatment. Concurrent outdoor new enclosure treatment inactivity levels showed a non-significant decrease and object manipulation and travelling were significantly greater than baseline levels suggesting increased activity, potentially explaining the corresponding increase in indoor inactivity. Environmental enrichment should, at the very least, challenge animals to maintain their physical strength (Young, 2003) and enriched naturalistic designs offer more physically challenging environments than do comparatively barren enclosures. Enrichment is known to increase activity levels of animals (Horses: Winskill *et al.*, 1996; Polar bears: Altman, 1999; Chimpanzees: Celli *et al.*, 2003; Frogs: Hurme *et al.*, 2003) and the chimpanzees may have experienced increased fatigue indoors during the new enclosure treatment due to increased activity in the outdoor enclosures at the same time.

The decreased self-directed behaviour during the orphans' indoor reconstruction treatment may have been the consequence of overlapping behaviour categories because self-directed behaviour and abnormal behaviour are not necessarily mutually exclusive of one another. Conflict behaviour in free living chimpanzees is often displaced in the form of a variety of self-directed behaviours, including self-scratching, rocking back and forth, masturbation and ineffective autogrooming (Wallace, 1979). Qualitative behavioural changes are associated with environmental changes (Clarke *et al.*, 1982a; Rumbaugh, 1988) and such changes in the intensity or frequency of self-directed behaviours leading to pathological consequences, such as self-scratching or grooming resulting in hair loss (Cooke & Schillaci, 2007), may result in them being reclassified as abnormal by observers.

In both the orphan and family groups, abnormal behaviour appeared to be important with regard to spatial change as both groups showed a significant increase in abnormal behaviour during the indoor reconstruction treatment. This was most likely a result of the spatial restriction experienced by the chimpanzees during the reconstruction period as alternative explanations are not satisfactory. In the case of the family group this may have been the result of construction noise, but two lines of evidence suggest that this is an unlikely explanation. Firstly, previous work on other species suggests that prolonged exposure to noise does not necessarily cause animals to be stressed. Giant pandas *Ailuropoda*

melanoleuca were relatively unaffected by demolition and construction noise from near their enclosure, only showing minor seasonally mediated cortisol elevation and increased stereotypy in only one individual (Powell *et al.*, 2006). Feeding in yellow baboons *Papio cynocephalus* was more stressful than prolonged exposure to industrial noise at levels over 100 dB at 2KHz, which did not invoke a significant stress response (Turkkan *et al.*, 1984). Secondly, habituation to noise is possible, resulting in a lowered stress response to noise over time (Babisch, 2003). The exposures of the pandas to the demolition and construction noise were over a three month period (Powell *et al.*, 2006) and the baboons eight hours a day for up to four months (Turkkan *et al.*, 1984), both showing some habituation to the noise. The construction period in my study lasted three months so it is likely that the family group also habituated to the noise of the reconstruction. Thus, the increase in abnormal behaviour in the family group is unlikely to have been a result of the construction noise near their enclosure.

In the orphan group, abnormal behaviour levels may have been related to the housing location. The animals were housed at the zoo hospital, an environment the animals may have associated with past stressful veterinary procedures as these may be a source of stress (Morgan & Tromborg, 2007). Thus, animals may learn to associate the veterinary environment with negative stimuli, exemplified by dogs which exhibit graded fear responses to veterinary examinations based on previous veterinary experiences (Döring *et al.*, 2009). However, as with the family group, the orphans were housed at the hospital for an extended period of time and thus are likely to have habituated to their environment, especially as they were not subjected to invasive or painful veterinary procedures during their time at the hospital, suggesting that the increased abnormal behaviour was more likely a product of the spatial restriction they experienced relative to their previous housing.

In both cases, it appears that the abnormal behaviour observed may have been more related to the crowding experienced under the reconstruction treatment. Both groups showed a significant increase in abnormal behaviour, suggesting that the physical environment played little role in this reaction. In addition, the sampling method used may have under-estimated levels of abnormal behaviour as instantaneous sampling is not the most effective method for recording brief behaviours (Martin & Bateson, 1986) such as hair plucking or self-injurious behaviour. Nonetheless, crowding itself is known to be stressful (Honess & Marin, 2006a; Morgan & Tromborg, 2007) and these results coupled with similar outcomes in other studies (Calhoun, 1962; Elton & Anderson, 1977; Clarke *et al.*, 1982b; Nieuwenhuijsen & de Waal, 1982; Judge *et al.*, 2006) suggest that abnormal behaviour may occur in animals as one of the outlets for the stress experienced under crowding. This evidence provides support for the

coping hypothesis (Rushen, 1993), suggesting that some abnormal behaviours function as a means of coping with stress. Concurrent physiological and behavioural measures of stress could be used in future studies to further investigate how abnormal behaviour functions in the context of spatial crowding in primates.

The lack of clear patterns seen in the indoor enclosure treatments in response to crowding may be related to the degree of crowding experienced by the chimpanzees, which experienced two changes in housing (space). Elton and Anderson (1977) reported on a gradual decrease in space in a group of olive baboons and found inconsistent changes in social behaviour with the reductions in space. Many have suggested that the strategy used by primates in response to crowding may be related to the amount of time spent under the crowding condition (Aureli *et al.*, 1995; Aureli & de Waal, 1997). In addition, the results of my study and those of Elton and Anderson (1977) suggest that the degree of crowding may also influence the behavioural responses primates exhibit to spatial crowding.

It is intriguing that the overall levels of social behaviour exhibited were very different between the two groups. The orphan group showed consistently lower levels of socio-positive behaviour and higher levels of inactivity than those of the family group. The orphan group had a 2:1 male biased sex ratio which may have resulted in lower levels of social bonding and social behaviour. High numbers of females within animal groups, as naturally occur in chimpanzee groups, is thought to promote stronger intra-sex bonding (Connor & Whitehead, 2005). Adult male chimpanzees are typically less social than adult females chimpanzees under captive conditions (Nieuwenhuijsen & de Waal, 1982; Pers. Obs.) and a similar crowding study reported lower levels of grooming and greater inter-individual spacing in all-male groups of green monkeys than mixed sex groups (Clarke & Mayeaux, 1992). In contrast to males, adult female chimpanzee tend to form larger grooming cliques involving more group members, than male-only cliques (Nakamura, 2003) and chimpanzee females appear to utilize affiliative interactions to minimize stress during periods of long-term crowding (Videan & Fritz, 2007). Thus, a lower number of females within the orphan group may have lead to lower recorded levels of social behaviour than in the family group.

The time spent in the respective groups may have also influenced the levels of recorded social interaction. The family group had been together in excess of 15 years whereas the orphan group had only been together for approximately six years at the time of the reconstruction. In addition, the orphan group were exposed to frequent introductions of new individuals during group formation. Social changes are associated with increased levels of aggression in Bolivian squirrel monkeys (Williams & Abee, 1988) and chimpanzees (Baker

et al., 2000). The histories of the individuals within the orphan group were not known but chimpanzees removed from their mothers at an early age exhibit poor social skills (Reimers *et al.*, 2007) and past experience is known to have an effect on primates responses to social manipulations (Honess & Marin, 2006a). Any abuse or maltreatment of the orphan individuals prior to their arrival at the Johannesburg Zoo would also be likely to have hindered their ability to form social bonds within the group. Novak *et al.* (1992) suggested that social cohesion and past experience may influence the responses of primates to environmental change and this study provides evidence to support this notion.

The procedure described in my study was initiated with welfare concerns in mind. Simple enrichments, such as novel objects (Brent & Stone, 1998) or feeding devices (Celli *et al.*, 2003) have been shown to be effective enrichment strategies for chimpanzees. Similarly, large-scale environmental change, as experienced by the chimpanzees in my study, have beneficial welfare outcomes for captive chimpanzees (Clarke *et al.*, 1982b), hanuman langurs *Presbytis entellus* (Little & Sommer, 2002) and callitrichid monkeys (Common marmosets *Callithrix jucchus* and cotton-top tamarins *Saguinus oedipus*: Chamove & Rohrhuber, 1989). Significantly lower levels of abnormal (in the family group only) and self-directed behaviour and higher levels of object manipulation and travel in the new enclosures suggest that both chimpanzee groups experienced better welfare in the new outdoor exhibits than in the old ones. Another important welfare effect of the change in enclosure is that both groups were recorded as 'hidden' more in the new enclosures than in the old enclosures. Visual isolation is important for captive chimpanzees (Bettinger *et al.*, 1994) and a lack of retreat space is considered a source of stress for captive animals (Morgan & Tromborg, 2007). However, whether the recorded changes reflect the motivations of the chimpanzees or merely difficulty in observing them is not clear.

From my results, it is clear that there is evidence to support both the tension-reduction and conflict-avoidance models of coping with spatial crowding while no support was found for the density-intensity model. The patterns observed here appear to be complicated by a variety of factors including novelty effects, energetic demands, past experience and social group cohesion. However, the results also suggest that abnormal behaviour may offer an alternative outlet for the stress experienced by primates under spatial crowding. Future studies should test whether abnormal behaviour is a realistic outlet for crowding stress and should focus on measuring physiological correlates of stress under these conditions.

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Chapter 3. Boxed in - Past spatial experience determines future spatial decisions in captive chimpanzees

Abstract

A common environmental enrichment practice in zoos is the redesign and reconstruction of enclosures from small, barren enclosures to larger, naturalistic enclosures. While apes are known to display distinct space use and environmental preferences, most evaluations of new enclosure efficacy have not explicitly investigated space use. The chimpanzee enclosure at the Johannesburg Zoo, South Africa, was remodelled and enlarged to 25x the original enclosure size in 2004, which provided the opportunity to investigate how the chimpanzees used the new space in relation to the previous housing five years after the reconstruction. The behaviour, space use and subgroup spacing patterns of the chimpanzees were recorded and examined in relation to various factors of the new enclosures as well as the dimensions of the previous enclosure (100 m^2). The chimpanzees displayed two patterns of spatial limitation. Firstly, space use was limited to the region of the enclosure which corresponds directly to the previous housing space. Secondly, the dimensions of subgroup formations matched the dimensions of their original housing on 98% of all observations. This pattern of subgroup spacing was non-random and is not explained by other candidate predictors such as social and thermal conditions and public interaction effects. The chimpanzees appear to display patterns of space use based on the dimensions and location of the previous enclosures. These patterns of space use appear to be a form of spatial learned helplessness, a spatio-cognitive deficit (SCD) resulting from the uncontrollable change in the spatial environment.

Introduction

Captive animals are frequently subject to uncontrollable, inappropriate conditions of both the social and physical environment (Judge & de Waal, 1993) which may compromise their welfare (Morgan & Tromborg, 2007). In response, redesign and reconstruction of enclosures to create more ‘naturalistic’ environments is often utilized as a form of environmental enrichment (Little & Sommer, 2002). These enclosures, typically comprising

elements of the natural environment, are designed to encourage natural behaviour (Novak et al., 1992).

Naturalistic enclosure designs are considered to be beneficial for animal welfare (Maple & Finlay, 1989; Ogden et al., 1990). Therefore, many studies have investigated the effects of such enclosure changes on behaviour, finding that naturalistic enclosures discourage abnormal behaviour and promote more natural behavioural patterns (Clarke et al., 1982; Novak et al., 1992). Animals frequently engage in novel behaviours (Chang et al., 1999) once released into naturalistic enclosures and readily engage with the novel substrates therein (Marriott & Meyers, 2005).

Providing captive animals with additional space is unlikely to be effective unless the space is used appropriately (Young, 2003) and thus there is a need to assess how animals transferred to new environments use the space provided. Post-occupancy evaluations of zoo enclosures seek to systematically determine the effectiveness of new enclosures in zoo environments with regard to the behavioural effects on animals, functionality for keepers and the perceptions of the public (Maple & Finlay, 1987; Kelling & Gaalema, 2011). Post-occupancy studies have been conducted on a variety of species, locations and enclosure types (e.g. Wilson et al., 2003). However, there are two aspects of post-occupancy evaluation that have been largely overlooked. Firstly, novelty is likely to initially influence behaviour in the new enclosures (Nash & Chilton, 1986; Ross et al., 2011a) but most studies have investigated behavioural changes relatively soon after release into the new enclosure. Secondly, despite the need for rigorous assessments of enclosure designs (Maple & Finlay, 1987; Kelling & Gaalema, 2011), post-occupancy evaluations have focused typically on abnormal behaviour (e.g. Little & Sommer, 2002) or visitor and caregiver perceptions of the design rather than the effect on the animals it houses (Wilson et al., 2003), with little focus on the space use of animals following a transfer to a new environment.

The type of enclosure in which an animal is housed will determine the space use of the animal (Wesley Burgess, 1980) but there is a prevailing assumption that animals will use enclosure spaces homogenously (evidenced by Clarke et al., 1982). However, space use in captivity is likely to be affected by intrinsic factors such as the enclosure size and structure as well as the social environment (Estevez & Christman, 2006). For example, the availability of shade is likely to influence behavioural thermoregulation (Barton et al., 1992). Moreover, much of animal spacing is governed by inter-individual distances and personal fields (McBride, 1971) and space use is therefore influenced by sociality (e.g. primates: McCowan et al., 2008). External factors, such as the presence of the visiting public in zoos, may

influence space use as well (Mallapur et al., 2005) and great apes in particular appear to prefer spaces where they receive human interactions (Ross & Lukas, 2006). Thus, the quality of an animal's enclosure may be more important than the quantity of space provided (Morgan & Tromborg, 2007) as particular environmental features may be important in driving space-use patterns.

One group of studies by Ross and colleagues have specifically examined the space use of apes in captivity, with regard to environmental complexity and size. Ross & Lukas (2006) examined the use of vertical tiers within an indoor exhibit by chimpanzees *Pan troglodytes* and Lowland gorillas *Gorilla gorilla gorilla* and found that both apes showed distinct preferences for particular tiers as well as particular physical features of the enclosure, including doorways and enclosure corners. Ross et al. (2009) applied electivity indices to examine how the same ape groups engaged with environmental features in a new housing condition, relating observed enclosure feature preferences to those displayed in a previous housing condition. They found that both chimpanzees and gorillas showed preferences for environmental features, but that some of the preferences appeared to be specific to particular enclosure designs (Ross et al., 2009). In a later study on the same subjects, the chimpanzees and gorillas effectively only used 3.2% and 1.5% of the three-dimensional space provided to them in an indoor-outdoor enclosure, suggesting that the apes were underusing the space provided (Ross et al., 2011b).

Studies of other primate species have highlighted similar patterns of limited space use. In one study, two groups of callitrichid monkeys (common marmosets Callithrix jacchus and cotton-top tamarins Saguinus oedipus respectively) were transferred from small enclosures (Marmosets: 3m x 2.1m x 1.4m; tamarins: 3m x 3.5m x 2.5m) to large outdoor areas (Marmosets: several square kilometres of open woodland; Tamarins: 45m x 27m outdoor enclosure; Chamove & Rohrhuber, 1989). Once released into their new enclosures, both groups displayed notably limited space use, particularly evident in the tamarins that spent almost all their time within 3m of their previous home cage, which was part of the new enclosure (Chamove & Rohrhuber, 1989). Similarly, in a study of space use in Lowland gorillas, two hand-reared individuals consistently displayed substantially more limited space use in a large outdoor enclosure at the Cincinnati Zoo than their wild-caught conspecifics(Hedeen, 1982; Hedeen, 1983).

It is curious that the tamarins described by Chamove & Rohrhuber (1989) remained approximately 3m from their home cage, the approximate dimensions of the floor area of their previous housing, as well as the fact that they remained close to their old home cage.

Furthermore, the gorillas described by Hedeen (1982; 1983) that had been reared in spatially limiting environments displayed notably limited space use when released into their larger outdoor enclosures whereas their wild-caught conspecifics did not display the same degree of limitation. Both of these examples suggest that primate space use may be influenced by past experience as well as the features of the current environment.

Based on the existing literature of primate post-occupancy space use, the works of Ross and colleagues and the outcomes of the studies of Chamove & Rohrhuber (1989) and Hedeen (1982; 1983), my study investigated the space use of a group of chimpanzees at the Johannesburg Zoo Ape House in 2009, approximately five years after the outdoor exhibit was remodelled to a naturalistic design in 2004, and relate the observed patterns of space use to the dimensions and location of the previous housing of the chimpanzees. The new enclosure was built in the location of the previous housing environment (see Chapter 2; Figure 1 below). I predicted that as chimpanzees appear to have distinct preferences for environmental features like doorways and corners (Ross & Lukas, 2006; Ross et al., 2009), areas of the enclosure that contained these features would be used more frequently than other areas. I also predicted that if the previous housing condition had affected the space use of the chimpanzees, in the same manner as described for the tamarins above (Chamove & Rohrhuber, 1989), the chimpanzees would use the area of the old enclosure more frequently than other areas.

Observations conducted during two other studies on the same group of chimpanzees (Chapters 4 & 5) suggested that the chimpanzees appeared to be limiting their group spacing patterns, forming consistently small subgroups despite the large available space (approximately 2 500m2). As such, my study also aimed to ascertain the subgroup spacing patterns of the chimpanzees at the Johannesburg Zoo Ape House and relate these patterns to features of the enclosure environment, including shade, visitor proximity, location within the enclosure and social interactions, and the previous housing condition.

Materials and Methods

Study subjects

The study subjects were a stable family group of chimpanzees, comprising four males (Thabu: 26 years; Yoda: 17 years; Amber: 10 years; Charles: 2 years) and four females (Daisy: 25 years; Zoe: 14 years; Lilly: 12 years; Joyce: 6 years). The group had been housed at the Johannesburg Zoo Ape House (hereafter referred to as the Ape House) since birth, with

the exception of one female, Lilly, who was originally part of a group of rescued orphan chimpanzees from central Africa and temporarily housed at the Ape House. She was introduced into the existing family group in 2005. Given that this study was conducted in 2009, the group had been together in excess of four years. Prior to this investigation, both chimpanzee groups were housed in a pair of outdoor enclosures with an area of 100m^2 each and an adjoining indoor night room (see Chapter 2). These enclosures were reconstructed and replaced by a large outdoor enclosure with an approximate total area of 2500m^2 (Figure 1).

Housing and husbandry

In the current study, the study subjects had access to a large outdoor enclosure (approximately 2500m^2; Figure 1), separated into two sections, approximately 1000m^2 and 1500m^2 respectively, by a dividing wall with a connecting doorway. The enclosure was surrounded, on most sides, by 8m high walls, capped with electrified fencing. All other sides were surrounded by 4-5m wide moats with 1m high electrified fencing along the edge of the moat and 30cm high fencing extending out of the water approximately 2m from the moat edge. Large trees, other vegetation, several large rocks and logs were located in both outdoor sections. The larger enclosure had a rock outcrop while the smaller enclosure had a three-panelled reinforced glass viewing window opposite the night room entrances as well as a large plastic barrel and tube chained to trees. Both outdoor enclosures offered free access to water at all times. Several felled trees were left in the enclosure as ‘natural’ climbing structures. Access to two indoor night rooms was provided through passages located in the rear walls of the outdoor enclosures. One of the two night rooms had a large wooden climbing apparatus, comprising several interconnected wooden beams, from which a thick rubberised hammock, a number of ropes and chains and a car tyre were suspended.

The feeding and husbandry regimes of the chimpanzees remained constant throughout the study. The chimpanzees were fed an assortment of foods twice daily and were provided free access to water at all times. Their morning feed was scattered randomly throughout their outdoor enclosures to encourage them to leave the night rooms and use the full available outdoor space. The chimpanzees had access to their outdoor enclosure between 10h00 and 15h00 (16h00 on weekends), during which time keepers and animal attendants cleaned the night rooms. Similarly, their afternoon feed was spread throughout the night rooms to encourage the chimpanzees to return indoors for the night.

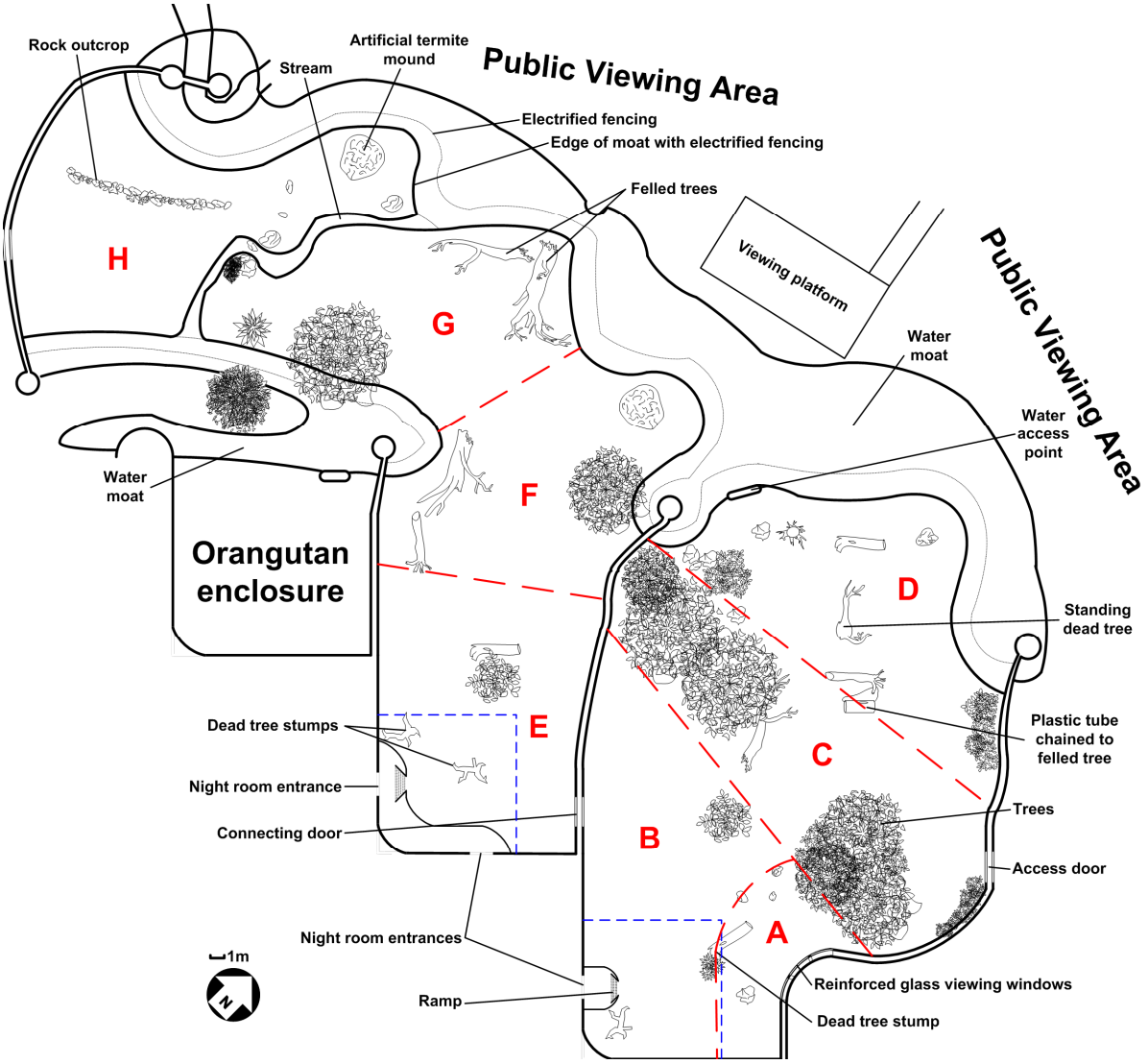

Figure 1. Outdoor housing area of the chimpanzee exhibit at the Johannesburg Zoo Ape House, South Africa, drawn to scale. Blue dashed lines denote the location and size of the original housing areas. Red dashed lines and large red letters denote zonation into eight unequally sized zones based on environmental elements, generalized patterns of shade availability, access to water and proximity to zoo visitors

Sampling technique

Observation sessions were carried out on 47 randomly selected days from March 2009 to July 2009. Observations were conducted between 10h00 and 16h00. During each sampling session, the behaviour of the chimpanzees was sampled for 60 minutes, using an instantaneous scan behaviour and spatial sampling technique (modified after Martin & Bateson, 1986). Samples were taken every five minutes and behaviour and space use data were recorded simultaneously. The resulting data consisted of a 12 behavioural sample and 12 spatial sample record per observation session. All behavioural data were recorded according to the categories described in Table 1. Observation sessions were classified into

three time categories: morning (10h00-11h59), midday (12h00-13h59) and afternoon (14h00-16h00).

Table 1. Definitions of behaviours sampled in the chimpanzee group at the Johannesburg Zoo, South Africa

Behaviour	***Definition***
Locomotion	Movement from one location to another, obviously not searching for food. Included walking, running and climbing
Foraging	Activity related to the searching for, manipulation or consumption of food or drink
Socio-negative	Chasing aggressively (characterised by sneering, open and closed grins and compressed lip faces. Usually associated with screams, barks and 'wraaa' calls; Goodall, 1986) or fighting with one another. Included aggressive gesturing or signalling. May be directed at the public as well
Socio-positive	Affiliative behaviours such as social grooming and embracing directed at other chimpanzees
Play	Social play (Wrestling, playful biting and playful chasing characterised by a relaxed face, possibly with a drooping lower lip, or a full play face. Usually silent but may include soft grunts or hoots; Goodall, 1986), object play (Play directed at or involving an inanimate object) and locomotor play (Solitary active play. Included running, rolling, swinging or somersaulting)
Inactivity	Resting, either standing or sitting down, or sleeping
Abnormal	Coprophagia/urophagia, self-mutilation, faeces throwing and hair plucking. Other behaviours were scored as abnormal based on the context in which they occurred and whether they occurred repetitively (>3 times in succession; Jones *et al.*, 2008). These included nipple pulling, abnormal gait and posturing and chronic masturbation
Public Interaction	Attempts by the chimpanzees to engage with the public through the viewing windows or fences
Hidden	Chimpanzees were obscured from view or behaviour was not identifiable according to the other categories listed

Spatial sampling

To improve accuracy, two spatial sampling methods were used to record the location of the chimpanzees in relation to the enclosure at each 5 minute time point: mapping and photography. Firstly, the relative positions of the chimpanzees were plotted on a scale map of the enclosure. Due to inaccuracies in the relative positions of environmental features such as trees and rocks on the maps, the relative distances between fixed landmarks in the enclosure were measured and used to correct positional information of chimpanzees on the maps. Only corrected points plotted on the maps were used in later analyses. Simultaneous to mapping and behavioural sampling, photographs of the respective chimpanzees were taken, using a Kodak C613 set at 3X optical zoom, which were used to examine subgroup compositions and to help ground-truth the mapping technique.

The mapping sampling technique was used to assess chimpanzee subgroups. A subgroup was defined as any collection of two or more chimpanzees within a 10m radius of one another. The 10m radius was used as this reflected the dimensions of the previous housing and little information exists on the spacing of natural chimpanzee groups. The influence of visual barriers were considered when deciding on the limits of subgroups and possible interactions with the public, based on the findings of Bettinger *et al.* (visual separation was found to be important in managing aggression and spacing in captive female chimpanzees: 1994). Thus, individuals outside of visual range of one another were not considered to be part of the same subgroup, regardless of the relative distances between the individuals concerned.

Excursions of individuals from subgroups were also recorded as any movement of an individual from and returning to the same subgroup that resulted in the individual exceeding a distance of 10m from other subgroup members for no more than five minutes. If the excursion exceeded five minutes (the time to the next sampling point), the individual was no longer considered to be part of its original subgroup and was not plotted on the map. However, excursions occurred rarely (< 3% of all observations) and were not considered for further analysis.

Enclosure space-use patterns

To assess the enclosure space-use patterns, the enclosure was divided into eight unequally sized zones based on environmental features, gross patterns of shade distribution, access to water and relative distances to the public. The zonation is shown in Figure 1. For time slots where the locations of all eight individuals were marked on the map, or could be determined by examining the photographs, zone use patterns were recorded. Only time slots where all eight chimpanzees were visible were used to ensure a full record of space use. Because photographs were used in addition to the maps to assess locations of the individuals, the recorded zone use patterns were used for subgroups and for individuals scattered about the enclosure. If two or more consecutive time slots within an observation session provided locations for all individuals, every second time slot was discarded, to minimize interdependence between time slots.

The resulting dataset of 82 time slots (approximately 6.8 hours of data) was then used to calculate the spread of participation index (SPI) using a modified equation for unequal zone size (Plowman, 2003). The index provides an estimate of space-use bias by generating a

value between 0 and 1, with 0 indicative of no space-use bias (all zones used equally) and 1 suggesting extreme bias (all observations in one zone). The SPI value for the chimpanzee data was 0.43, suggesting a moderate degree of space-use bias, and so space-use was interrogated further (see Data analysis).

Subgroup spacing patterns

If the previous experience of the group in their smaller old enclosure was a potential factor influencing the spacing of the chimpanzees, one would expect that they would limit their subgroup spacing to dimensions smaller than or equal to those of their previous housing conditions. Based on this assumption, the subgroup formations were classified according to whether they were within or exceeded the original dimensions of their enclosure (a 10m x 10m square; refer to Figure 1) with a 1m edge effect, resulting in a 11 x 11m block. Thus subgroups were compared against an 11m x 11m block. All classifications were based on the two-dimensional space occupation of the subgroups, such that individuals in elevated positions, such as trees, were still considered part of subgroups on the ground below them, provided they were in visual contact. If the subgroup fell within the 11m x 11m block it was labelled as a 'small subgroup', otherwise if a subgroup extended beyond the 11m x 11m block, it was labelled as a 'large subgroup'.

Proximity of chimpanzees to the public is thought to influence chimpanzee behaviour (Pederson *et al.*, 2005) which might have influenced subgroup formation patterns. Similarly, chimpanzees may use estimates of inter-individual distance to determine group spacing. For this reason, for all subgroups, the sum of the inter-individual distances of those chimpanzees on the periphery of the group, with an additional 1m edge effect (referred to as the 'subgroup polygon'), minimum inter-individual distance, maximum inter-individual distance and minimum distance to the public were recorded. In addition, given the structural differences between the two enclosure sections, I recorded which of the sections the subgroup occurred in and what proportion of the space (with a 1m edge effect), of the relevant section the subgroup occupied.

It is also possible that the observed patterns of subgroup spacing may be the result of the thermal conditions experienced by the chimpanzees in particular areas of the enclosure. Thus, the weather conditions (sunny, cloudy or overcast), the time of day when behaviours were sampled (morning, midday or afternoon) and the maximum temperature for that day were recorded. The degree of available shade in the enclosure was also recorded at the start

of the observation session by visually estimating the percentage of the enclosure that was shaded at the start of the session and classifying the degree of shade according to a 5-point scale (1: 0-25% shade; 2: 25-50% shade; 3: 50-75% shade; 4: 75-100% shade; 5: overcast). Furthermore, to provide an estimate of the potentially experienced thermal conditions, each subgroup formed was assigned a value according to the following index:

$$I_s = \frac{S}{D + S}$$

where *S* is the number of individuals in the shade and *D* is the number of individuals in direct sunlight. Individuals were considered to be in shade if any part of their trunk was shaded. These measures of shade and sun utilization were then compared to the subgroup size categories for each time slot. Overcast days were excluded from this analysis so as to minimize bias toward shade utilization, resulting in the omission of four days from the final analyses.

Social influences on subgroup spacing

In order to determine whether social factors might be governing subgroup spacing, the individual composition of subgroups was assessed. Photographs were used to identify individuals wherever possible to generate a record of subgroup composition. All possible pair associations were scored per subgroup, such that each subgroup composition was summarised as a number of pairwise inter-individual associations.

In addition to recording which chimpanzees formed subgroups, I recorded the individuals that were not part of the respective subgroups. Thus, for every observation session a matrix was generated with the number of times that every possible pair combination of individuals occurred within a subgroup and the number of times that each pair was not part of a subgroup.

Data analysis

All analyses were conducted using Statistica 7 (StatSoft, 2008) unless otherwise stated. All tests were two-tailed and test significance was set at 0.05.

For all generalized linear model (GLZ) analyses, response variable states were mutually exclusive (e.g. a subgroup either fits within a 10m x 10m space or does not;

therefore, it is either a large subgroup, or a small one, but cannot be both simultaneously), and as such were coded as counts of the two states (e.g. small or large subgroups) of the variable in question. This resulted in a binomial presence/absence count for each variable. As the data were coded as binary response variables, generalized linear models were used because they do not assume a normal distribution (Crawley, 2007). This binomial presence/absence structure was then used as the response variable in the GLZ analyses.

Enclosure space use

Following calculation of the spread of participation index (SPI), space-use patterns were examined by comparing the observed and expected frequencies of zone use for all time periods (morning, midday, afternoon). Expected frequencies were calculated based on the area of each zone, assuming homogenous space use. Zone size was calculated using the scale map and SimplePCI software (Compix). For both observed and expected frequencies, the number of hits (number of times an individual was present in the zone) and misses (number of times an individual was not present in the zone) were calculated. In addition to the statistical analysis described below, zone bias was calculated, for all the data pooled and for individual time periods, by subtracting the expected hits from the observed hits and was plotted graphically (Appendix 1 and Appendix 2).

Space-use records were analysed using a GLZ with a binomial error structure and logit link function. The time of day (morning, midday, afternoon), zone (A-H; Figure 2) and frequency type (observed, expected) were used as categorical predictors, while the binomial counts of hits and misses per zone was used as the response variable. In order to directly address the aims of the study, only the appropriate second-order and third-order interaction effects were examined in detail. Significant differences within the second-order and third-order effects were identified through β-estimate coefficients and confidence intervals and are reported as significant for $p \leq 0.05$.

Subgroup spacing null model

To determine whether the number of small subgroups was random, I generated a randomized null model using Monte Carlo sequences and compared this to the number of observed small subgroups. The comparison was done through a 1000 iteration randomization test. The outcome of the randomization test suggested that the observed subgroups formation

was not random. In addition, I ran a χ^2 test to analyse whether the occurrence of small and large subgroups differed from chance.

Behavioural effects on subgroup spacing

The behaviour of an individual may influence the formation of subgroups of a particular size. For example, behaviours such as allo-grooming require close spacing and thus a small subgroup formation is more likely to occur when subgroup members engage in such activities. Alternatively, behaviours such as travelling are not likely to encourage tight spacing as this might hinder movement. Thus, in order to establish whether particular behaviours were driving the formation of small and large subgroups, I used a GLZ with a logit link function and binomial error structure. The behaviour (Table 1) was used as the categorical predictor and the counts of occurrences of that behaviour in small and large subgroups was coded as the binomial dependent (absent/present) response variable. β-estimate coefficients and confidence limits were used to assess specific differences between first order (behaviour) effects and are reported as significant for $p \leq 0.05$.

Environmental effects on subgroup spacing

The effects of environmental and spatial factors on subgroup spacing patterns were examined using a backward-stepwise GLZ with a logit link function and binomial error structure. The variables examined were assigned according to Table 2. β-estimate coefficients and confidence limits were used to assess specific differences between first order (time of day, section of enclosure, subgroup type) and second order (time of day*section of enclosure, section of enclosure*subgroup type, time of day*subgroup type) effects and are reported as significant at $p \leq 0.05$. Significant continuous predictors were correlated to subgroup size using a Spearman's Rank Order Correlation.

Social effects on subgroup spacing

The data on pair formations were examined to assess social pair associations and non-associations which might drive the formation of tightly spaced subgroups. First, a cellwise comparison using adjusted residuals in MatMan^{TM} was run to identify social associations. Following this, five significant social pair associations were identified (i.e. individuals that participated in subgroups more frequently than expected by chance alone; Daisy: Joyce; Daisy: Zoe; Daisy: Lilly; Zoe: Charles; Zoe: Joyce; hereafter referred to as 'key

associations') and 14 social pair non-associations (i.e. individuals that participated together in subgroups less frequently than expected by chance alone; Thabu: Daisy; Thabu: Joyce; Thabu: Charles; Daisy: Yoda; Yoda: Joyce; Yoda: Charles; Yoda: Lilly; Yoda: Amber; Yoda: Zoe; Zoe: Lilly; Zoe: Amber; Lilly: Amber; Amber: Joyce; Amber: Charles). Based on the identified key associations, I performed a series of two-tailed χ^2 tests to assess the number of times a pair was part of any sized subgroup compared to; i) the number of times they could have been part of a subgroup, and ii) the times subgroups formed, regardless of subgroup size in both cases.

Table 2. Factor distribution for the backward-stepwise Generalized Linear Model used to investigate potential influences on subgroup formation in a group of chimpanzees at the Johannesburg Zoo, South Africa

Categorical Predictor Variables	Dependent Variable	Continuous Predictor Variables
Time of day (Morning; Midday; Afternoon)	Subgroup type (Small; Large)	Weather conditions at start of session (Clear or Cloudy; Overcast days were excluded from analyses to minimize bias toward shade utilization)
		Maximum daily temperature
		Percentage available shade in enclosure at start of session
Section of enclosure		Shade index
		Minimum distance to the public
		Maximum inter-individual distance
		Minimum inter-individual distance
		Subgroup polygon (With 1m edge effect)
		Proportion of enclosure section area used

In order to determine whether key associations might predict the formation of small subgroups specifically, we then ran a series of two-tailed χ^2 tests to examine the following relationship:

$$\frac{Key\ Association\ (Small\ Subgroups : Large\ Subgroups)}{All\ subgroup\ formations\ (Small\ Subgroups : Large\ Subgroups)}$$

For example, if a total of 14 small subgroups and 3 large subgroups are recorded, while 6 of the small subgroups and 2 of the large subgroup formations involve key associations, a comparison of the 6:2 key association subgroups and the 14:3 total subgroups was then analysed using a χ^2 test. This would suggest whether the proportion of small: large subgroups

involving key associations differed to the overall proportion of small: large subgroups, regardless of which individuals participated.

Results

Space use

Time of day (Wald $\chi^2_2 = 15.13$; $p < 0.001$), enclosure zone (Wald $\chi^2_7 = 230.05$; $p < 0.001$) and frequency type (Wald $\chi^2_1 = 38.97$; $p < 0.001$) were all significant predictors of zone use patterns. In addition, the time of day*enclosure zone (Wald $\chi^2_{14} = 112.88$; $p < 0.001$), time of day*frequency type (Wald $\chi^2_2 = 15.11$; $p < 0.001$) and enclosure zone*frequency type (Wald $\chi^2_7 = 221.23$; $p < 0.001$; Figure 2) interaction effects were significant predictors of the zone use patterns. Zones A and B were significantly overutilised while zones D – H were significantly underutilised in relation to the expected patterns of zone use based on the area of each zone (Figure 3). The time of day*enclosure zone*frequency type (Wald $\chi^2_{14} = 111.6$; $p < 0.001$; Figure 3) was also a significant predictor of the model outcomes with zones E, G and H significantly underutilised in the morning, zones E and H significantly underutilised around midday and zones C, D, F, G and H significantly underutilised in the afternoon. Zones A and B were significantly overutilised both at midday and in the afternoon (Figure 4).

Null model and subgroup size

The results of the Monte Carlo sequence null model randomization test showed that the observed patterns of subgroup formation were not random ($p < 0.0001$). The resulting *p*-value is considered significant because it is not greater than the level of significance ($\alpha = 0.050$) of the model (Onghena & Edgington, 1994), and thus the null hypothesis of no difference between the treatments (small, < 11m x 11m, and large, > 11m x 11m, subgroups) is rejected. In addition, significantly more small subgroups (1254 small subgroups) formed than large subgroups (31 large subgroups; $\chi^2_1 = 752.26$; $p < 0.0001$).

Behaviour

Behaviour was not a significant predictor of subgroup type (Wald $\chi^2_7 = 0.059$; $p = 1.000$; Figure 4), indicating that behaviours that encouraged or required smaller inter-individual distances, such as socio-positive interactions, like allogrooming, were not likely to influence subgroup spacing.

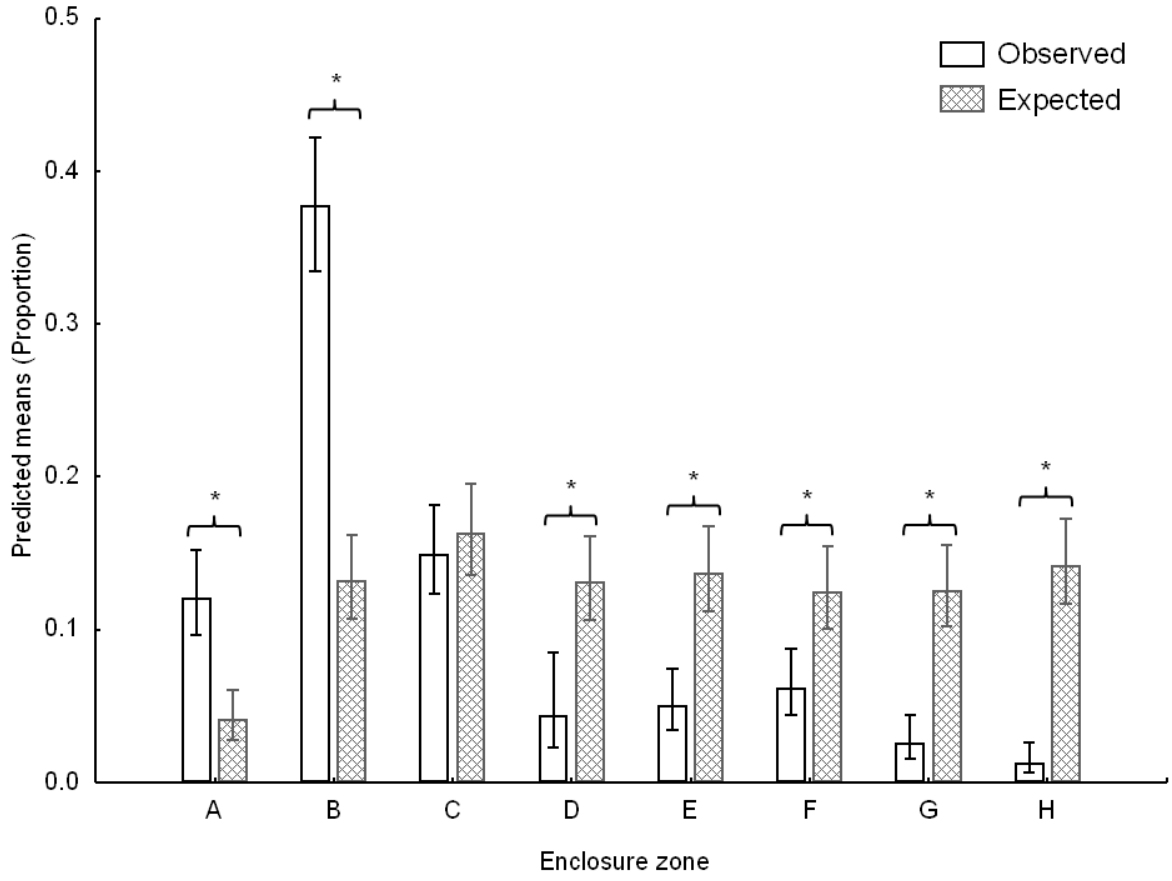

Figure 2. Observed and expected frequencies of zone use for eight zones in the chimpanzee enclosure at the Johannesburg Zoo Ape House, South Africa. Bars denote predicted means proportions while whiskers denote confidence limits. Stars and brackets above bars denote significant ($p < 0.05$) differences between observed and expected zone use

Environmental and space factors

Time of day, section of enclosure and time of day*section of enclosure interaction were not good predictors of subgroup size (Table 3). None of the continuous predictor variables were significant predictors of subgroup size with the exception of subgroup polygon, which was weakly positively associated with increasing subgroup size (Spearman's Rank Order correlation: R = 0.218; $p < 0.05$) and minimum distance to the public, which was weakly negatively associated with increasing subgroup size (Spearman's Rank Order correlation: R = -0.114; $p < 0.05$; Table 3).

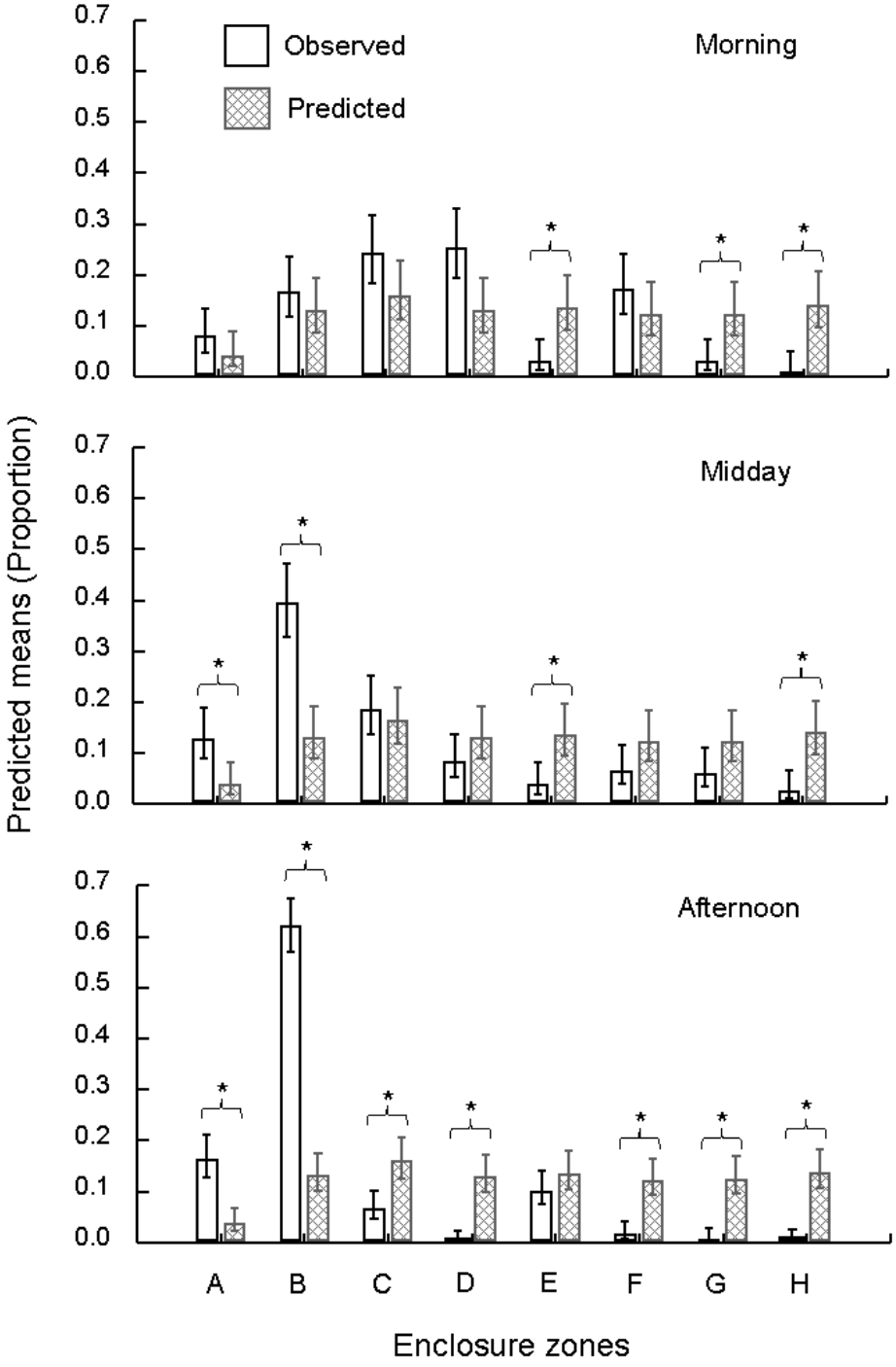

Figure 3. Zone use patterns for the chimpanzees at the Johannesburg Zoo Ape House, South Africa. Patterns of space use are represented for three time periods. Bars denote predicted means proportions for hits and misses in each zone while whiskers denote confidence intervals. Stars and brackets denote significant differences ($p < 0.05$) between observed and expected counts

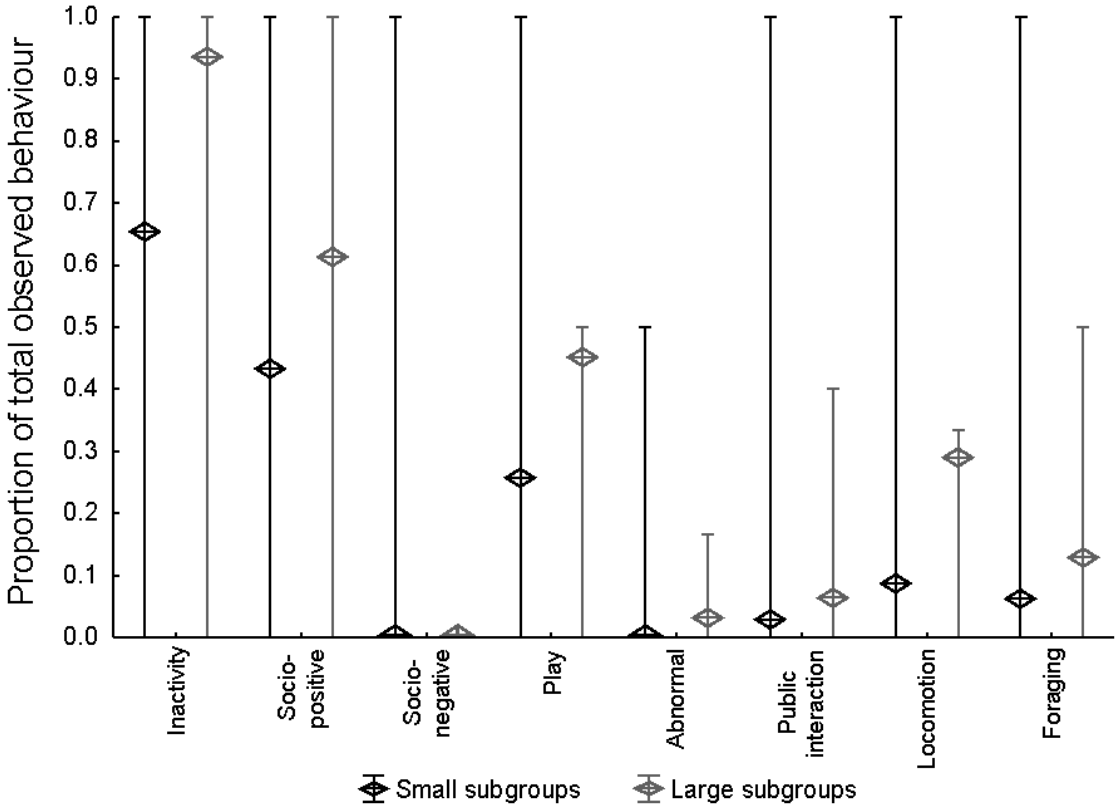

Figure 4. Proportions of observed behaviour levels in small (< 11m x 11m) and large (> 11m x 11m) chimpanzee subgroups at the Johannesburg Zoo, South Africa. Diamonds denote overall behaviour proportions while whiskers denote minimum and maximum behaviour proportions respectively

Table 3. The output of a GLZ analysis, showing the effects of categorical and continuous predictors listed for the assessment of subgroup size for chimpanzees at the Johannesburg Zoo, South Africa. Variables and test statistics in bold indicate significant predictors of subgroup type. Statistics = Wald χ^2

	Parameters	***Statistics***
Categorical Predictors	Time of day	$\chi^2_2 = 0.128$; $p = 0.938$
	Section of enclosure	$\chi^2_1 = 0.01$; $p = 0.997$
	Time of day*Section of enclosure	$\chi^2_2 = 0.931$; $p = 0.628$
Continuous Predictor Variables	Weather conditions at start of session	$\chi^2_1 = 3.240$; $p = 0.072$
	Maximum daily temperature	$\chi^2_1 = 0.993$; $p = 0.319$
	Percentage available shade in enclosure at start of session	$\chi^2_1 = 0.604$; $p = 0.437$
	Shade index	$\chi^2_1 = 0.541$; $p = 0.462$
	Minimum distance to the public	**$\chi^2_1 = 5.114$; $p = 0.024$**
	Maximum inter-individual distance	$\chi^2_1 = 1.137$; $p = 0.286$
	Minimum inter-individual distance	$\chi^2_1 = 0.040$; $p = 0.841$
	Subgroup polygon (With 1m edge effect)	**$\chi^2_1 = 3.963$; $p = 0.047$**
	Proportion of enclosure section area used	$\chi^2_1 = 1.232$; $p = 0.267$

Social influences on subgroup formation and spacing

Five significant pair associations and 14 significant pair non-associations were identified (χ^2_{41} = 1437.33; Table 4). For the five key associations, the proportion of total subgroups that formed was significantly different to the proportion of subgroups in which the pair participated (Daisy: Joyce χ^2_1 = 44.54, $p < 0.001$; Daisy: Zoe χ^2_1 = 39.54, $p < 0.001$; Daisy: Lilly χ^2_1 = 29.16, $p < 0.001$; Zoe: Charles χ^2_1 = 34.97, $p < 0.001$; Zoe: Joyce χ^2_1 = 31.84, $p < 0.001$). Thus, the frequency of participation in small subgroups by key associations did not match the frequency of small subgroup formations, indicating that key association pair participation was not a good predictor of subgroup formation.

With the exception of one pair (Zoe: Charles; χ^2_1 = 3.61, p = 0.057), the proportion of small to large subgroups involving key associations was significantly different from the overall small to large subgroup formations (Daisy: Joyce χ^2_1 = 5.53, p = 0.019; Daisy: Zoe χ^2_1 = 8.53, p = 0.004; Daisy: Lilly χ^2_1 = 25.7, $p < 0.001$; Zoe: Joyce χ^2_1 = 10.96, $p < 0.001$). This suggests that the proportion of small to large subgroups that involved Zoe: Charles was similar to the overall proportion of small to large subgroup formations.

Table 4. Z statistics for a χ^2 using adjusted residuals used to examine associations between specific pairs of chimpanzees at the Johannesburg Zoo, South Africa. Bold Z values within grey cells denote significant interactions and superscripts denote level of significance ($^1 p < 0.05$; $^2 p < 0.01$; $^3 p < 0.001$)

		Non-associations (Pairs that formed less frequently than expected by chance)							
		Daisy	*Thabu*	*Joyce*	*Charles*	*Yoda*	*Amber*	*Lilly*	*Zoe*
Associations (Pairs that formed more frequently than expected by chance)	*Daisy*		**14.41^3**	-1.29	0.10	**2.94^2**	-0.48	-3.51	-8.61
	Thabu	-9.85		**11.07^3**	**9.42^3**	-0.76	-2.54	-2.60	-3.49
	Joyce	**4.15^3**	-9.46		1.98	**4.90^3**	**2.55^1**	-0.90	-3.76
	Charles	1.55	-8.57	-1.10		**6.43^3**	**3.34^2**	1.35	-4.24
	Yoda	-4.63	0.47	-6.83	-8.28		**7.86^3**	**3.15^2**	**5.11^3**
	Amber	-1.33	1.69	-5.08	-5.61	-8.47		**7.79^3**	**8.55^3**
	Lilly	**2.15^2**	0.18	-1.24	-3.90	-2.79	-6.02		**10.70^3**
	Zoe	**10.75^3**	1.51	**3.24^2**	**4.63^3**	-5.23	-6.77	-4.86	

Discussion

My study aimed to examine the long-term effects of a change of enclosure, from a small (100m^2), barren enclosure to a large (2500m^2), naturalistic enclosure, on the space use and spacing patterns of a group of captive chimpanzees at the Johannesburg Zoo. The first part of this study examined how the chimpanzees used the space in the new enclosure by quantifying the number of times the chimpanzees were observed in each of eight zones and

comparing the observations to expected frequencies of zone use based on zone size. I found that the chimpanzees did not use the space homogenously, showing a preference for zones A and B. Space use also appeared to vary with time of day, with the most evenly distributed space use occurring in the morning, but midday and afternoon periods were significantly biased toward zones A and B, with all other zones being underused.

The chimpanzees biased space use to the zones in the vicinity of the original 10m x 10m enclosures (see Figure 1). When the chimpanzees were initially released into the new enclosures, the group that is currently housed at the zoo was housed on the side of the enclosure with zones A-D and this may explain why the chimpanzees preferentially use A and B over E. Previous spatial environments appear to influence future patterns of space use in gorillas (Hedeen, 1982; Hedeen, 1983) and callitrichid monkeys (Chamove & Rohrhuber, 1989), and it appears that a similar effect may be influencing the enclosure use patterns of the chimpanzees. Because the daily feed for the chimpanzees was scattered throughout the outdoor enclosure sections, it is unlikely that the location of food influenced the space use of the chimpanzees. In addition, food was provided in the morning during which time the chimpanzees displayed the most unrestricted space use, yet the periods when the bias for zones A and B was most pronounced was during the midday and afternoon periods (non-feeding times). I consider two other interpretations of the data below, but neither appear to sufficiently explain the observed pattern of bias in space use within the enclosure.

On the one hand, the patterns of space use appear to conform to my prediction that the chimpanzees would use spaces associated with doorways and corners more than other areas. Previous studies have found that chimpanzees exhibit a preference for these areas (Ross & Lukas, 2006; Ross et al., 2009), and zone B has two doorways: a night room entrance and the interconnecting doorway between the two enclosure sections. However, zone E has a similar structure to zones A and B but has three doorways (two night room and one interconnecting), and was consistently underused, suggesting that perhaps the attraction to doorways and corners does not explain the overuse of zones A and B.

One the other hand, captive apes prefer areas where they can engage in human interaction (Ross & Lukas, 2006), which they may experience as enriching (Morgan & Tromborg, 2007; but see: Wells, 2005; Carder & Semple, 2008). If visitor presence is enriching, then chimpanzees may be attracted to zone A as the large windows in the wall at that location offered opportunities for close interactions between the chimpanzees and zoo visitors and workers alike. However, this does not explain the overuse of zone B nor does it explain why zones D, F, G and H, zones with extensive interactive and visual access to the

public, were underutilized. Also, if the chimpanzees found visitor interactions stressful, one would expect that neither A nor B would be overused as both provide open, constant visual access to zoo visitors. Furthermore, zone B provides little cover to the chimpanzees and chimpanzees are known to avoid open areas (Ross *et al.*, 2009), suggesting that some other aspect of the space is driving the observed pattern.

I also investigated the patterns of subgroup spacing displayed by the chimpanzees following observations that the chimpanzees appeared to consistently form small subgroups in the large outdoor enclosure. The formation of tightly spaced, small subgroups (< 11m x 11m) was found to be non-random, with significantly more small than large (> 11m x 11m) subgroups forming, which was not predicted by observed behaviour, time of day, enclosure section, maximum daily temperature, shade availability, the proportion of the total available space being used or the maximum and minimum inter-individual distances.

Minimum distance to the public and subgroup polygon were identified as significant predictors of subgroup spacing patterns but do not appear to explain the observed patterns of subgroup spacing. Subgroup polygon was weakly positively associated with subgroup size while the minimum distance to the public but, logically, as subgroups form over a small area, they are more inclined to have a smaller polygon. Thus, the relationship between these factors does little to clarify the causality of small subgroup formation.

Interestingly, the minimum distance to the public is weakly negatively associated with subgroup size, such that when the chimpanzees were close to the public, they formed subgroups over a larger area. Interactions with zoo visitors are seen as vital to further interests of zoos (Hosey, 2005), but evidence from a variety of studies suggests that such interactions with the public are stressful for non-human primates (Fernandez *et al.*, 2009). Yet, chimpanzees will voluntarily interact with the public for extended periods (Cook & Hosey, 1995) and readily exchange objects with humans (Hyatt & Hopkins, 1998), suggesting that these interactions are not necessarily as stressful for chimpanzees as for other non-human captive primates. The chimpanzees at the Johannesburg Zoo interacted with the public infrequently (2.5% of all observed behaviour), suggesting that this behaviour is not a likely driver of subgroup spacing.

However, public interactions were usually through begging behaviour and I suggest that the formation of larger subgroups during such interactions could function to reduce inter-individual competition for food. Widely distributed resources are associated with lower aggression levels (Honess & Marin, 2006) whereas restricted access to food can cause increased aggression (Southwick, 1967) and thus the chimpanzees may increase their inter-

individual spacing as a means of minimizing potential conflict. In nature, spacing and territoriality in free-living chimpanzees appears to be driven by food dispersal and resource competition (Williams *et al.*, 2004) with subgroups forming in response to dispersed (Wittenberger, 1981) but not abundant resources (Doran, 1997).

When social factors were examined, none of the social pair associations of chimpanzees in my study were good predictors of subgroup formations and only one pair of individuals (Zoe: Charles) participated in small:large subgroup formations at a similar proportion as overall small:large subgroup formations. While at first this suggests that the presence of this pair might drive small subgroup spacing, the fact that no pairs were associated with overall patterns of subgroup formation precludes this possibility. In addition, the Zoe: Charles subgroups (small - 228: large - 11) occurred at similar proportions to overall small:large subgroup formations (small – 1254: large – 31), but more small subgroups formed in the absence of this pair than when they were present. Primate biology predicts that sociality might determine spacing patterns as primate societies are maintained through complex dominance hierarchies (Judge & de Waal, 1997) and primates generally ascribe great value to their social relationships (de Waal, 1989). In addition, animal spacing patterns tend to be governed by individual-specific rules regarding personal space (McBride, 1971) and a study of macaques *Macaca mulatta* found that social factors accounted for the spacing patterns of first to second nearest neighbours (Wesley Burgess, 1980). Thus it is curious that social factors did not explain the subgroup spacing of the chimpanzees.

Previous work on enclosure changes indicated that chimpanzees will not underuse the new enclosures (Clarke *et al.*, 1982) but little information exists on spacing patterns in free-ranging chimpanzee groups in the literature. However, free-ranging chimpanzees typically have large inter-individual distances (Jane Goodall, Pers. Comm.) and studies of free-ranging populations have considered chimpanzees to be in the same subgroup with inter-individual distances of between 35m (Bates & Byrne, 2009) and 100m (Wrangham & Smuts, 1980), considerably larger than the observed patterns at the Johannesburg Zoo.

Thus, in the absence of more obvious explanations, I propose a novel interpretation for my findings. It occurs to me that the spatial behaviour of the chimpanzees resembles a form of learned helplessness. Learned helplessness (LH) is the inability of a subject to overcome a deferred controllable stressor following exposure to an uncontrollable stressor (Petty *et al.*, 1994). The LH hypothesis suggests that when the reaction of an individual to a stimulus fails to generate an effect, it learns that the resulting outcomes are independent of its actions (Overmier & Seligman, 1967; Seligman *et al.*, 1968) which then impedes learning

that the response and outcomes are linked (Maier & Seligman, 1976) when an influence over the outcomes is possible (Maier, 1984). The emergence of the LH effect appears to be contingent upon the initial stimulus being uncontrollable (Seligman *et al.*, 1968), regardless of whether the initial stimulus is benign, neutral or noxious (Seligman, 1972; Maier & Seligman, 1976; Maier, 1980; Maier, 1984).

LH has been characterised by three criteria: 1) a failure to react appropriately to a stimulus, 2) difficulty learning that the individual's responses to future stimuli may influence the events, and 3) that these two effects arise only under conditions where the initial stimulus is uncontrollable and when the stimulus is controllable (Seligman, 1972; Seligman & Beagley, 1975). Evaluating my data against these criteria points toward a learned helplessness explanation. With regard to the first criterion, the chimpanzees displayed consistently tight subgroup spacing as well as a tendency to use the zones in the vicinity to the original enclosure, despite the availability of a large space, similar to the escape failures described for dogs (Seligman & Maier, 1967) and rats (Musty *et al.*, 1990). This type of reaction suggests an inability to learn that the previous experience, limited available space and associated restrictions on space use and subgroup spacing in this case, no longer applies in the larger enclosure, fulfilling the second criterion. Controllability of the initial stimulus is crucial to the onset of LH (Overmier & Seligman, 1967; Seligman & Maier, 1967; Seligman *et al.*, 1968; Seligman, 1972; Maier, 1984; Petty *et al.*, 1994; Maier, 2001) but it was impossible to generate a 'controllable' spatial change of this type for the chimpanzee group, and thus, the third criterion (above) cannot be explicitly confirmed for the chimpanzee group. However, the enclosure change was uncontrollable for the chimpanzees and thus, based on existing LH literature, the chimpanzees appear to meet the criteria for LH (personal correspondence with Martin Seligman).

Curiously, the space-use bias and tight spacing patterns of the chimpanzees occurred despite the fact that the larger enclosure was not a deferred noxious stimulus. One might argue that the chimpanzees experienced the large space as stressful, but they readily travelled independently of one another throughout the enclosure and the new enclosure had persistent ameliorating effects on various stress-related behaviours immediately after, and 10 weeks following, the release into the new enclosures (Chapter 2), suggesting that the new enclosures were not overtly stressful. Instead, my study suggests that the experience of the chimpanzees in the previous restricted housing had limited their perception of the space available to them, resulting in, what I term, a spatio-cognitive deficit (SCD). This SCD may be a previous undescribed manifestation of LH, which requires no noxious stimulus for the LH effect to be

evident. The SCD described here in the chimpanzees mirrors anecdotal descriptions of LH in pike (pike placed into a tank with guppies, but separated from the guppies by a glass barrier, failed to move through the full tank when the barrier was removed; Beasor, 2006) and fleas (fleas placed into a closed jar initially jump but soon stop, having learned the physical limits on their locomotion due to the jar lid; Ziglar, 2005), as well as patterns of spatial limitation in other primate species (Hedeen, 1982; Hedeen, 1983; Chamove & Rohrhuber, 1989).

In conclusion, the chimpanzees at the Johannesburg Zoo limited their space use in their outdoor enclosure to areas in the vicinity of their previous housing and formed tightly spaced subgroups in the enlarged enclosure that are not explained by several candidate predictors. The observed patterns of spatial limitation resemble the effects of learned helplessness. These results may have important implications for captive animal welfare and conservation, particularly when animals are transferred to larger cages for enrichment or relocated into nature, as occurs in many rehabilitation and re-release programs.

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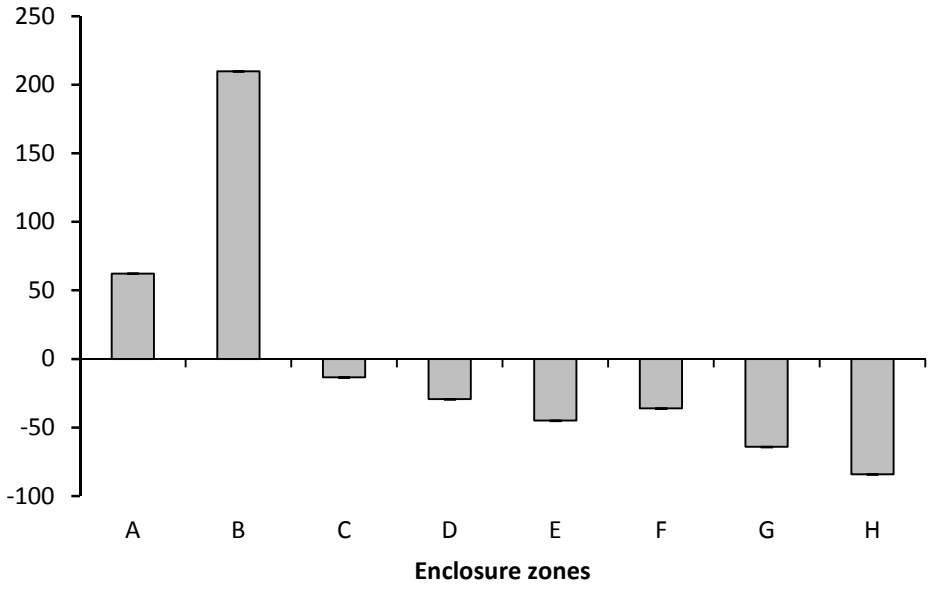
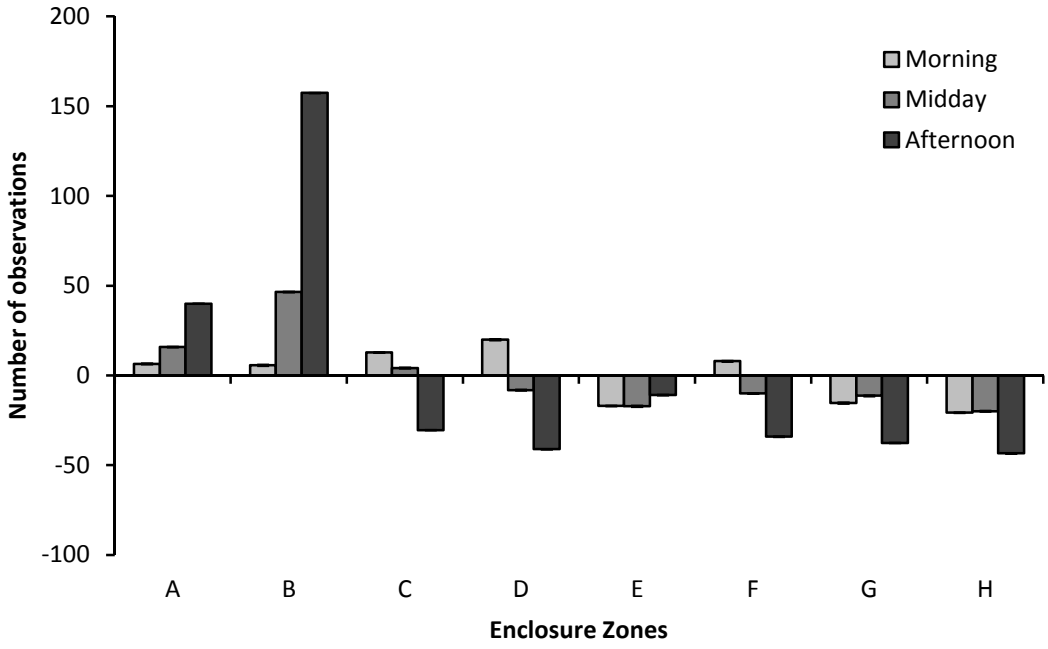
Appendices: Space-use bias of a group of captive chimpanzees at Johannesburg Zoo



Appendix 1. Overall patterns of bias in the space use of a group of captive chimpanzee at the Johannesburg Zoo, South Africa. Letters below the horizontal axis refer to eight unequal-sized zones based on environmental elements, generalized patterns of shade availability, access to water and proximity to zoo visitors. Bars indicate space-use bias, calculated by subtracting expected frequencies of zone use from observed frequencies. Bars with values above the horizontal axis indicate an overuse of a zone, while bars below the axis indicate an underuse of the zone. Whiskers denote standard error for the observed frequencies of space use



Appendix 2. Patterns of bias in the space use of a group of captive chimpanzee during three time periods (morning, midday and afternoon) at the Johannesburg Zoo, South Africa. Letters below the horizontal axis refer to eight unequal-sized zones based on environmental elements, generalized patterns of shade availability, access to water and proximity to zoo visitors. Bars indicate space-use bias, calculated by subtracting expected frequencies of zone use from observed frequencies. Bars with values above the horizontal axis indicate an overuse of a zone, while bars below the axis indicate an underuse of the zone. Whiskers denote standard error for the observed frequencies of space use

Chapter 4. Chimpanzee responses to imposed social change in captivity

Abstract

The fission-fusion nature of chimpanzee society subjects individuals to frequent changes in the social environment. Social changes may compromise existing social organisation, particularly when change is frequent. Individual emigration and party reunion following separation are commonplace in free-living chimpanzee populations but their effect on overall behaviour and socio-dynamics remains untested. This study aimed to examine the effect of two similar treatments (the merging of groups following a period of separation and the removal of an adult female from an existing group) on the behaviour of a group of captive chimpanzees. Both treatments were associated with increased socio-positive behaviour and decreased or unchanged aggressive behaviour. The inter-individual associations of the chimpanzees were altered by both treatments but the removal of an adult female appears to have been less stressful than the merging of two groups. These experiments provide a case study of how such social change influences chimpanzee social dynamics.

Introduction

Under natural conditions, chimpanzees *Pan troglodytes* are highly social, living within multi-male multi-female fission-fusion groups (Rowe, 1996; Dunbar & Barrett, 2000; Vigilant, 2004). These groups, called ‘communities’ (Sakura, 1994), occupy large home ranges, which are aggressively defended and patrolled by male coalitions (Williams *et al.*, 2002). Males are philopatric whereas females disperse (Mitani *et al.*, 2002), occasionally migrating between communities after dispersal (Wittenberger, 1981) based on individual female social development and the energetic consequences of emigration (Stumpf *et al.*, 2009).

Within communities, chimpanzees form small sub-groups or ‘parties’ which vary in size and composition (Mitani & Watts, 2005) as well as duration (Bates & Byrne, 2009). In many species, animals form groups in response to resource availability, with individuals joining or leaving groups according to the costs or benefits thereof (Estevez *et al.*, 2007).

Chimpanzee party formation specifically, appears to be linked to a variety of factors and parties may form for the purposes of feeding and resting (Doran, 1997), boundary patrolling (Mitani & Watts, 2005) or group safety (Sakura, 1994).

Most free-ranging primate species are subject to such changes through demographic processes, including individual migration between groups (Olsson & Westlund, 2007) which can induce a degree of social instability (Honess & Marin, 2006). Chimpanzees are no exception and the socio-dynamics of chimpanzee society result in individuals experiencing frequent changes in group size and composition. Changes in the social environment, particularly the arrival of unfamiliar individuals to existing groups (Morgan & Tromborg, 2007), are likely to elicit aggression (Eaton *et al.*, 1981) and free-ranging chimpanzee parties typically react to unfamiliar intruders with aggression (Boesch, 2003). However, due to highly variable party composition where individuals have considerable freedom to associate with various conspecifics (Gilby & Wrangham, 2008), chimpanzees may retain knowledge regarding relative inter-individual relationships (Aureli *et al.*, 2008), suggesting that selective reactions to individuals may underlie the responses of chimpanzee parties to familiar and unfamiliar conspecifics.

Periods of social disruption place individuals at risk of physical injury (Baker *et al.*, 2000) and studies in captive environments suggest that such social changes also induce psychological stress, especially in primates (Honess & Marin, 2006). While primates naturally experience social instability and the associated stress and aggression, in captivity, unnatural social conditions (Morgan & Tromborg, 2007), frequent social change (Clarke & Mayeaux, 1992), which is a common husbandry practice (Visalberghi & Anderson, 1993), and inappropriate socio-spatial conditions, such as a lack of retreat space (Price, 1999), may exacerbate the effects of social change on levels of aggression (Clarke & Mayeaux, 1992). Aggression forms part of normal primate interactions, but the management of aggression and injury risk can become a serious welfare concern in captivity (Baker *et al.*, 2000; McCowan *et al.*, 2008), and while alteration of stable captive primate groups is discouraged (Olsson & Westlund, 2007), manipulations of the social environment may become necessary in captivity.

While aggression is often an outcome of social disruption, primates may also engage in non-agonistic interactions during such disruptions. Primates ascribe great value to their social relationships (de Waal, 1989) and utilize social play (Palagi *et al.*, 2004; Tacconi & Palagi, 2009), grooming (Henzi *et al.*, 2003) and close physical contact (Schino & Troisi, 1990) as well as gestures such as mounting, kissing or hugging (Wallace, 1979) as means of

maintaining these relationships and placating would-be aggressors, a functional pattern of behaviour formalized by the relationship-repair hypothesis (*sensu* Cords & Aureli, 1996). Such behaviours serve to reduce tension within the group (Honess & Marin, 2006; Tacconi & Palagi, 2009) and may be selectively employed during periods of social disruption (Judge *et al.*, 2006).

A number of studies have examined primate responses to social change, mostly in the form of introducing unfamiliar individuals to existing groups, with mixed outcomes. Campbell's monkeys *Cercopithecus campbelli campbelli* exhibited elevated aggression between, but limited socio-positive interactions to within, matrilines in response to the removal of two females (Lemasson *et al.*, 2005). Bolivian Squirrel monkeys *Saimiri boliviensis boliviensis* exhibited age- and sex-specific aggression responses to, and received significantly higher levels of submissive behaviour from, unfamiliar introduced individuals (Williams & Abee, 1988) while Rhesus monkeys *Macaca mulatta* displayed elevated aggression in response to the introduction of unfamiliar individuals of various age and sex classes (Southwick, 1967). Artificial rank-reversal in Japanese macaques *Macaca fuscata* caused increased aggression by dominants and increased submission by subordinates while dominance relationships remained stable following restoration of normal group composition (Chapais & Larose, 1988).

To date, few studies have examined the behavioural responses of captive chimpanzees to social disturbance. Captive chimpanzees appear to display patterns of both social and non-social behaviour similar to those of their free-ranging counterparts (King *et al.*, 1980), suggesting that behavioural responses to social disturbance would be similar as well. One investigation of social disturbance, in the form of conflict and reconciliation behaviour in captive chimpanzees described a complex interaction of consolation, affiliation and redirection behaviours in response to conflict (Fuentes *et al.*, 2002), while Koyama *et al.* (2006) describe a system of affiliation both in anticipation of, and in response to, conflict in captive chimpanzees. However, these examples offer little clarification with regard to how chimpanzees respond to the frequent acute social disruption which characterises chimpanzee society. To the best of my knowledge, only one study has examined short-term responses of chimpanzees to the reintroduction of familiar conspecifics following separation (Okamoto *et al.*, 2001), but the influence of such events on long-term behaviour remains unknown. Thus, my study poses and investigates the following questions: How do chimpanzees react to the return of familiar conspecifics after a period of separation? How do chimpanzees react to an individual leaving an existing stable social group?

The aim of this study was to examine the effects of two distinct social disruptions on the behaviour of a group of captive chimpanzees. I examined two distinct social manipulations in a group of captive chimpanzees at the Johannesburg Zoo. Both manipulations, including all housing and social conditions, were prescribed by zoo management and staff and carried out accordingly. The first manipulation involved the fission of the chimpanzee group into two groups (an all-male and a female and juvenile group respectively) for the purposes of introducing a hand-reared juvenile. My study focused on the behaviour and socio-dynamics of these two groups when separated, and then after merging (defined as '…when two or more established [primate] groups are brought together', Honess & Marin, 2006, pg 404). The second manipulation involved the effect of the removal of an individual adult female from the group on behaviour and socio-dynamics.

Based on the existing primate literature, I predicted that social disruptions would be associated with increased agonistic interactions and increased stress-related behaviours. Increased affiliative social interactions might also be expected along with changes in the social interactions of the group(s).

Materials and Methods

Study subjects and experimental procedures

Experiment 1: Group merging

The study subjects were a socially housed group of chimpanzees at the Ape House at the Johannesburg Zoo, South Africa. The chimpanzee group studied consisted of five males (Thabu: 24 years; Yoda: 16 years; Amber: 9 years; Joshua: 1 year; Charles: 1 year) and five females (Daisy: 24 years; Zoe: 13 years; Lilly: 16 years; Claudette: 12 years; Joyce: 5 years). Yoda, Zoe, Amber, Joyce and Charles were the progeny of Thabu and Daisy, while Lilly and Claudette were introduced to the group approximately four years prior, with the group composition remaining stable for four years. Joshua, Claudette's son, was hand-reared and was to be introduced into the main chimpanzee group. For the purposes of his introduction to the group, the males and females were housed separately (Separated treatment), with females occupying section 1 and males section 2 of the outdoor enclosures (described in detail later; see fig. 1) as mandated by management at the Johannesburg Zoo. Infants were housed with the females (the group of females and juveniles is hereafter referred to as 'female group').

After approximately four months, the two groups were combined (Merged treatment), allowing both groups to interact and giving them access to both sections of the enclosure. During the introduction, Joshua was killed by two males.

Experiment 2: Individual removal

The group composition was similar to the Group merging experiment (four males: Thabu, Yoda, Amber and Charles; five females: Daisy, Zoe, Lilly, Claudette, Joyce). At the time, zoo management suspected that Claudette was the target of unilateral aggression from the other chimpanzees, a common problem in captive (Visalberghi & Anderson, 1993) and free-ranging (Nishida *et al.*, 1995) primates. Following my observations of the group for approximately two months (Claudette Present treatment), Claudette was removed from the group for transfer to the Jane Goodall Institute South Africa Chimpanzee Eden, a chimpanzee sanctuary located approximately 400 km away from the Johannesburg Zoo. Following her removal from the group, Claudette was housed in an indoor enclosure while the group was housed in two of the indoor-outdoor enclosures, allowing them access to both sections of the outdoor enclosure (Claudette Absent treatment). I observed the group under this condition for approximately two months.

Housing and husbandry

For both experiments, the chimpanzees were housed at the Johannesburg Zoo Ape House, an indoor-outdoor exhibit (Figure 1). The chimpanzees were given 5-6 hour access to an outdoor enclosure daily, between 10h00 and 15h00 on weekdays and between 10h00 and 16h00 on weekends. The outdoor enclosure was divided into two adjacent sections (section 1: 1000m^2; section 2: 1500m^2), connected with a doorway through the dividing wall and each with large trees, other vegetation, rocks and felled trees for climbing. Each section was bordered by 8m high walls topped with electric fencing on most sides. All other sides were surrounded with 4-5m wide moats bordered by 1m high electric fencing and with 30cm high electric fencing extending out of the water approximately 2m into the moat. Section 1 had a three-panelled reinforced glass viewing window opposite the night room entrances, located at the rear of each section.

The chimpanzees were fed a variety of fresh fruit and vegetables, as well as primate pellets and boiled egg, twice daily. The first feed was scattered randomly throughout the outdoor enclosures to encourage foraging and as incentive for the chimpanzees to leave their

night rooms. The second feed was scattered randomly throughout the night rooms to encourage the chimpanzees to return to the night rooms. Water was provided *ad libitum* in all conditions, through drinking troughs or access to the moat in both enclosure sections.

Behavioural observation

Group merging

Both the male and female groups were observed under the separated treatment for approximately two months from February 2008. No observations were conducted for 8 weeks between treatments, during which time Joshua was killed, to accommodate the zoo management schedule for the merging. Observations in the merged treatment started in late May 2008, approximately 2 weeks after the death of Joshua, and ended in July 2008.

Individual removal

Observations of the group were conducted for approximately 2 months in each condition (Claudette present: starting July 2008; Claudette removed: starting November 2008).

Sampling technique

For both studies (group merging and removal), an instantaneous focal animal sampling technique similar to that described by Martin & Bateson (1986) was used, which consisted of a one minute inter-sample interval for the group merging study and a 30 second inter-sample interval for the individual removal study, for a full hour. In the group merging study, it was logistically easier to observe at a 1min sample interval due to the two groups being housed in separate enclosure sections. For both studies, observation sessions were spread evenly across 5 hours (1 hour a day over 5 non-consecutive days) between 10h00 to 15h00 for each individual chimpanzee in each treatment, covering the time that they were in their outdoor enclosures only. Thus, for each experiment a total of 10 hours of data were recorded per chimpanzee, resulting in a total of 80 hours of data in both the group merging experiment and the individual removal experiment. The behaviour categories scored are listed in Table 1.

For group merging, both infants were excluded from the scoring due to the fact that at the start of the study, Charles was relatively immobile, still strongly dependent and engaging

in ventral-ventral contact with his mother, and Joshua's death meant that observations for Joshua would have been unbalanced. Claudette was not included as a focal subject in the individual removal experiment as she was to be removed, but Charles was included as a focal subject because he was more mobile and interacted with other chimpanzees often.

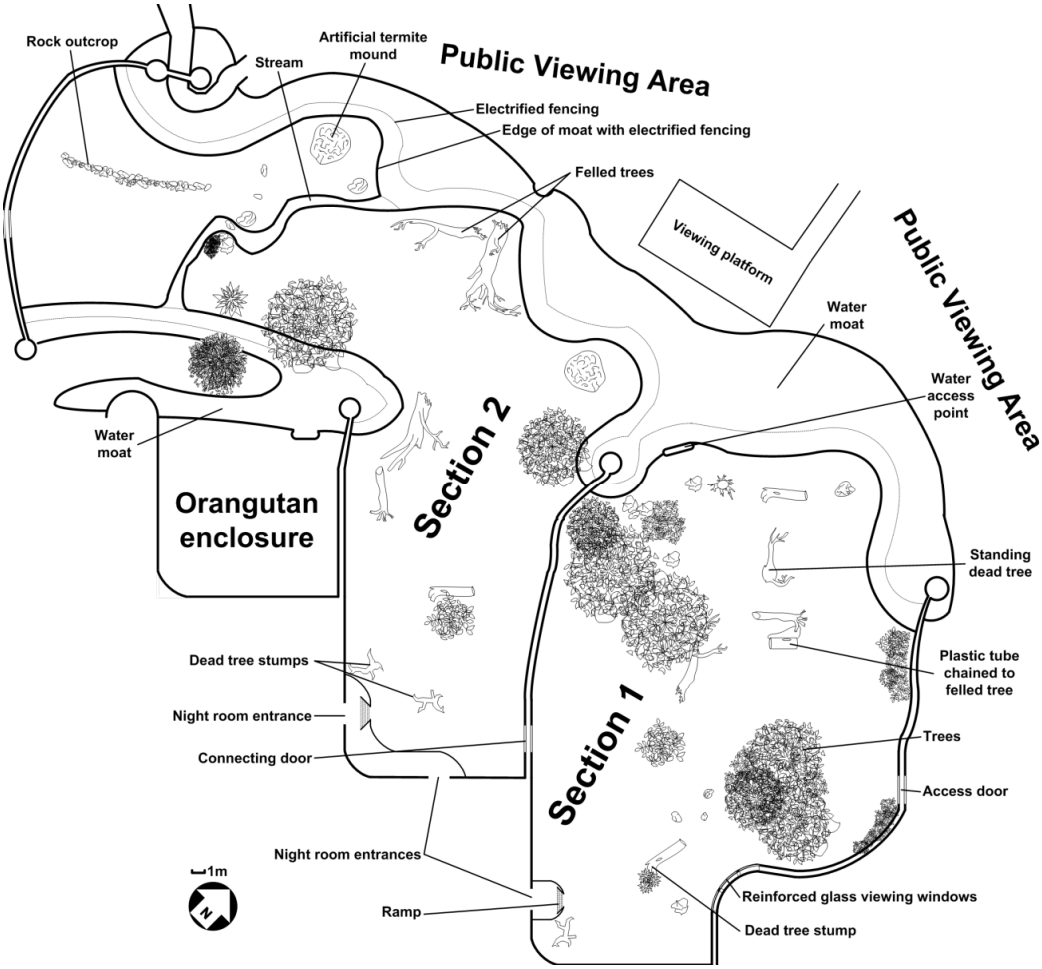


Figure 1. Outdoor housing area of the chimpanzee exhibit at the Johannesburg Zoo Ape House, South Africa, drawn to scale.

For the group merging experiment, interactions with the public were included in the 'Other' category but following completion of the observations for the group merging, it became apparent that interactions with the zoo visitors were a frequent occurrence. 'Public Interaction' was included in the behavioural scoring in the individual removal experiment in addition to the existing categories from the group merging (Table 1). Wood (1998) noted that primates frequently interact with zoo visitors and will often direct aggression at zoo visitors (Mitchell *et al.*, 1991). Evidence from various studies suggests visitor presence may be

stressful for captive primates (Chamove *et al.*, 1988; Todd *et al.*, 2007; Fernandez *et al.*, 2009), including chimpanzees (Maki *et al.*, 1987).

For all social behaviours scored, the individuals involved and which individuals received or directed interactions (directionality) between individuals were recorded. While the behaviours of the infants were not scored, all interactions with them by focal individuals were recorded.

Data analysis

Overall patterns of behaviour

Analyses of overall patterns of behaviour were conducted using Statistica 7 (StatSoft, 2008). For all tests, the model significance was set at $\alpha = 0.05$ and analyses were two-tailed.

Group merging

A Variance Components Analysis (VCA) was initially used to examine the influence of Group (i.e. male group; female group) as a categorical predictor of behaviour. Group was not found to be a significant categorical predictor of behaviour ($F_{1,48} = 3.876$; $p = 0.094$) and was thus not considered further.

'Vocalising' was not observed and not considered further. The 'Being Groomed' and 'Grooming Others' behaviour categories were combined into a new category 'Social Grooming' as specific social interactions were examined in detail later. 'Aggression' occurred approximately 0.14% of all recorded behaviour and was thus incorporated into the 'Other' category for the generalized linear model (GLZ) analyses, described below.

In order to examine the treatment effects on overall behaviour, a GLZ was used with a binomial distribution and a logit link function. As the behaviours scored were mutually exclusive (the expression of one behaviour often precludes the expression of another), behaviour was coded as counts of the absence and presence of a behaviour, resulting in a binomial absence/presence count for each behaviour. The binomial presence/absence structure was used as the response variable in the GLZ while the categorical predictors included treatment (separated; merged) and behaviour. β-estimate coefficients were used to assess specific differences between first order (treatment; behaviour) and second order (treatment*behaviour) effects and are reported as significant for $p \leq 0.05$. In order to

specifically address the aims of the study, first order effects were not examined in detail but second order effects were.

In order to examine treatment effects on levels of aggression, aggression data from both groups was pooled and a Fisher's exact test was conducted on the pooled aggression data. In all cases, observed counts of aggression were compared to total counts of all other behaviours, for both the separated and merged treatments.

Individual removal

As with the group merging experiment, 'Vocalizing' was excluded from further analyses, and 'Being Groomed' and 'Grooming Others' were combined into 'Social Grooming' and 'Aggression' occurred only 0.02% of all observed behaviour and was incorporated into 'Other' and later analysed using a Fisher's exact test.

A GLZ with a binomial distribution and a logit link function was used to investigate the effects of the removal of Claudette on group behaviour. The categorical predictors used included treatment (Claudette present; Claudette absent) and behaviour, while a coded binomial presence/absence structure of the behaviour counts was the response variable. Specific differences between first order (treatment; behaviour) and second order (treatment*behaviour) effects were assessed through β-estimate coefficients and are reported as significant for $p \leq 0.05$. As with the group merging study, only second order effects were examined in detail.

A Fisher's exact test, similar to that used in Group Merging, was also used to examine treatment effects on levels of aggression. The observed counts of aggression were compared to total counts of all other behaviours, for both the Claudette present and Claudette absent treatments.

Social interactions

For both experiments, specific interactions were excluded from the analyses. In Group Merging, interactions with the juveniles were excluded on the basis that they were incomplete measures of social interaction for those individuals, as Charles was too young to be mobile, which limited in his interactions with others, and Joshua was killed half-way through the experiment. Similarly, in Individual Removal, interactions with Claudette were excluded on the basis that she was absent in the Claudette removed treatment.

Table 1. Definitions of behaviours observed in the chimpanzee groups at the Johannesburg Zoo, South Africa, to assess the effects of two distinct social changes

Behaviour	***Definition***
Travelling	Movement from one location to another, obviously not searching for food. Included walking, running and climbing
Foraging	Searching for, manipulating or consuming food or drink.
Vigilance	When the animals ceased other activities in order to monitor or observe their surroundings or other individuals
Inactivity	Resting, either standing, sitting or lying down. Included sleeping
Abnormal	Coprophagia/urophagia, self-mutilation, faeces throwing and hair plucking. Other behaviours were scored as abnormal based on the context in which they occurred and whether they occurred repetitively (>3 times in succession; Jones *et al.*, 2008). These included nipple pulling, abnormal gait and posturing and chronic masturbation
Aggression	Chasing aggressively (characterised by sneering, open and closed grins and compressed lip faces. Usually associated with screams, barks and 'wraaa' calls; Goodall, 1986) or fighting with one another. Included aggressive gesturing or signalling
Social play	Wrestling, playful biting and playful chasing (characterised by a relaxed face, possibly with a drooping lower lip, or a full play face. Usually silent but may include soft grunts or hoots; Goodall, 1986)
Object play	Play directed at or involving an inanimate object
Locomotor play	Solitary active play. Included running, rolling, swinging or somersaulting
Self-grooming	Licking, cleaning, picking at and removing items from their own skin or hair. Included self-scratching
Being groomed	When individuals made no effort to engage in other activities in order to be licked, cleaned or have items from the skin or hair removed by others
Grooming others	Licking, cleaning and removing items from the skin or hair of others
Vocalising	When the chimpanzees generated a sound through their voice
Public interaction (Individual Removal only)	Any interaction with zoo visitors by the chimpanzees. Included displays, play and begging gestures and throwing objects at visitors
Other	Any identifiable behaviour that didn't obviously fit into the other behaviour categories
Hidden	Chimpanzees were obscured from view or behaviour was not identifiable according to the other categories listed

In order to examine quantitative changes in social associations, pooled interactions (both directed at and received by others) for focal subjects were examined using cell-wise comparisons with adjusted residuals and a χ^2 analysis in MatMan^{TM} (Ballintijn *et al.*, 2003). These interactions were used to highlight associations that occurred at levels above and below those expected by chance.

Qualitative changes in association were examined according to the following index of affiliation:

$$I_A = \left(\frac{T_{2\,(x:y)}}{T_{2\,(\Sigma x)}}\right) - \left(\frac{T_{1(x:y)}}{T_{1\,(\Sigma x)}}\right)$$

Where $T_{(x:y)}$ refers to the number of interactions initiated by individual *x* (the focal individual) at recipient *y*. $T_{(\Sigma x)}$ refers to the sum total interactions initiated by individual *x* to any recipient within the group, including individual *y* and all other individuals. As separate indices were calculated for the group merging and individual removal experiments, the numerical subscripts denote whether the measures are for the first (Separated treatment for the group merging study; Claudette present treatment for the individual removal study) or second (Merged treatment for the group merging study; Claudette absent treatment for the individual removal study) treatments respectively. In the event that an individual displayed no interactions throughout a given treatment, the relevant value in the equation (e.g. $T_{1(x:y)}$ / $T_{1(\Sigma x)}$) was set to zero. The index generates values that range on a scale from positive to negative 1, with negative 1 indicating a complete reversal of relationship in a negative direction (always associating → never associating), an output of positive 1 indicating a reversal in a positive direction (never associating → always associating) and 0 indicating no change at all from separated to merged (Group Merging) and from Claudette present to Claudette absent (Individual Removal). Interactions for which individuals were not present were not considered.

Results

Overall patterns of behaviour

Group merging

When examining the overall treatment effects on behaviour, treatment (Wald χ^2_1 = 5.28; p = 0.022) was found to be a significant predictor of the model outcomes with the separated and merged treatments significantly different to one another. Behaviour (Wald χ^2_{11} = 3498.32; $p < 0.005$) was also found to be a good predictor of the model outcomes. The treatment*behaviour interaction effect (Wald χ^2_{11} = 314.21; $p < 0.005$) was also significant in predicting model outcomes (Figure 2). Abnormal behaviour, self-grooming and social

grooming levels and 'hidden' were all significantly greater during the merged group treatment, whereas foraging and inactivity levels were significantly lower in comparison to the separate group treatment.

There were low levels of aggression before (8 of out 2392 observations) and after (0 our of 2400 observations) merger of the groups, yet a Fisher's exact indicated a significant ($p = 0.013$) decrease in aggression.

Individual removal

Both treatment (Wald $\chi^2_1 = 40.3$; $p < 0.001$) and behaviour (Wald $\chi^2_{12} = 6018.59$; $p < 0.001$) were significant predictors of the model outcomes. The treatment*behaviour interaction (Wald $\chi^2_{12} = 520.03$; $p < 0.001$; Figure 3) also significantly predicted the model outcomes. Following Claudette's removal, levels of social grooming, public interaction, 'Other' and 'Hidden' increased significantly with concurrent significant decreases in foraging, vigilance and inactivity. No significant change in levels of abnormal behaviour, play or self-grooming occurred.

Aggression levels were low and there was no significant change in aggression levels ($p = 0.249$; Fisher's exact test) from the Claudette present (2/478 observations) to Claudette absent (0/480 observations) treatments.

Social interactions

Group merging

A number of significant associations emerged for pooled associations regardless of whether received or directed ($\chi^2_{41} = 371.71$; Z statistics and corresponding p values presented in Table 2; raw data in Appendices 1 & 2). Males formed only one significant association prior to merging of the groups (Thabu: Yoda; Table 2). There were four significant positive (greater than chance) associations among the females prior to merging (Claudette: Lilly; Daisy: Zoe; Daisy: Joyce; Zoe: Lilly) and three significant negative (lower than chance) associations (Claudette: Daisy; Zoe: Claudette; Zoe: Joyce). Following merging, many of the female-female associations remained the same or became more frequent than predicted by chance while all three male-male associations became significant positive associations. Six significant male-female associations emerged following merging (Thabu: Daisy; Thabu: Zoe; Daisy: Yoda; Zoe: Amber; Lilly: Amber; Claudette: Amber; Table 2).

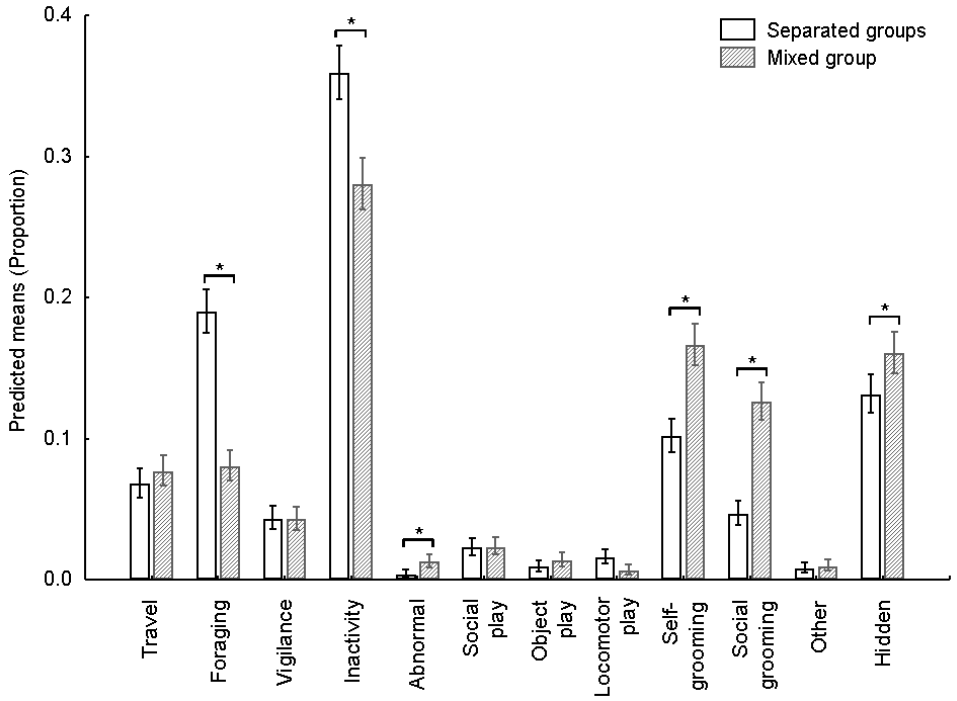


Figure 2. Relative changes in levels of selected behaviours observed in a group of chimpanzees at the Johannesburg Zoo, South Africa, housed separately as two groups and when combined into a single group. Whiskers denote confidence limits while bars denote respective predicted mean proportions of the total observed behaviour for each behaviour category for each treatment. Stars above the bars indicate significant differences ($p < 0.05$)

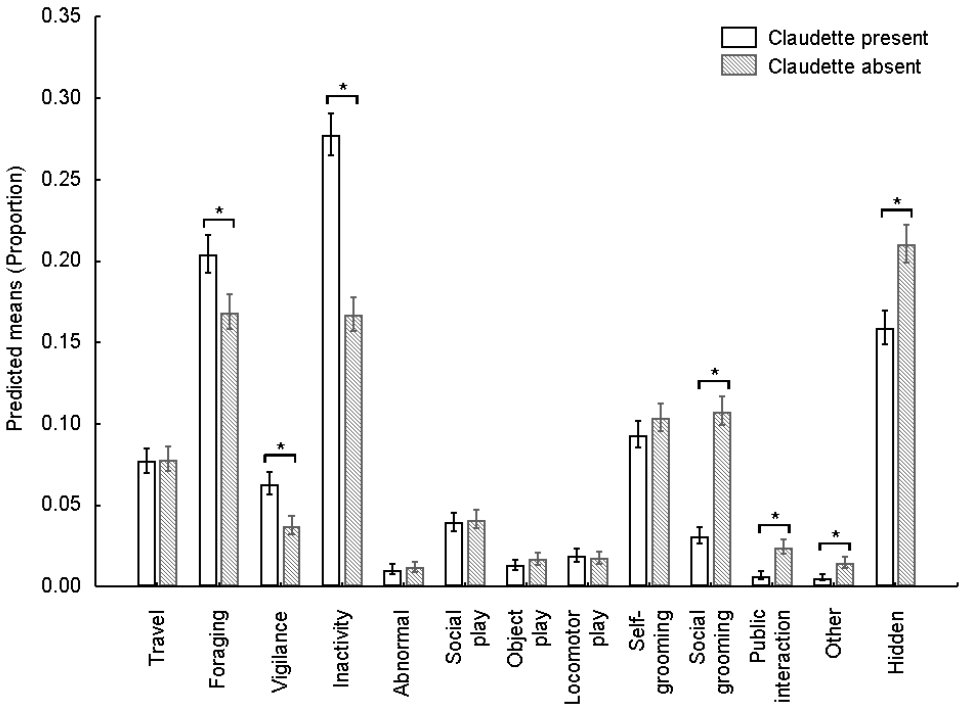


Figure 3. Relative changes in levels of selected behaviours observed in a group of chimpanzees at the Johannesburg Zoo, South Africa, following the removal of a single adult female (Claudette) from the group. Whiskers denote confidence limits while bars denote respective predicted mean proportions of the total observed behaviour for each behaviour category for each respective treatment. Stars above the bars indicate significant differences ($p < 0.05$)

Various qualitative changes in association were noted following merging of the groups (Table 3) but patterns of changing association were neither clear nor predictable. Both tables 2 and 3 show selective changes in association that appear to be individual-specific and do not generalise to age/sex/dominance classes. The greatest decrease in association amongst the males was seen in the interactions by Yoda (dominant male) directed at his father, Thabu. Amongst females, the greatest reduction in association was interactions by Lilly (dominant female) directed at Daisy, an unrelated female. Among the males, the greatest increase in association was seen in interactions by Yoda directed at his sister, Zoe. Among females, Joyce displayed the greatest increase in interactions, directing all her interactions to her brother Amber.

Individual removal

A number of significant associations emerged for both treatments (χ^2_{41} = 1415.56; Z statistics and corresponding *p* values presented in Table 4; raw data in Appendices 3 & 4). Prior to Claudette's removal, four significant positive (greater than chance) pair associations were found (Daisy: Joyce; Daisy: Charles; Yoda: Lilly; Joyce: Charles) in addition to 16 significant negative (lower than chance) associations (Table 4). However, after Claudette's removal, for pairs that displayed any significant association, nine associations became more positive and four more negative. No clear age/sex related patterns of change in association emerged.

Table 2. Z statistics for χ^2 tests using adjusted residuals used to examine specific chimpanzee pair associations at the Johannesburg Zoo, South Africa, before and after the merging of two groups. Bold Z values in grey cells denote significant interactions and subscripts denote level of significance ($_3$ $p < 0.001$; $_2$ $p < 0.01$; $_1$ $p < 0.05$). Individuals are listed in order of decreasing age with the dominant male highlighted with a star (*) and dominant female highlighted with a hash (#)

		Groups Separated							
		Thabu	**Daisy**	**Yoda***	**Zoe**	**Lilly#**	**Claudette**	**Amber**	**Joyce**
Groups Merged	**Thabu**		0.46	**5.27$_3$**	**-3.48$_3$**	**-3.12$_2$**	-0.48	**2.17$_1$**	**4.46$_3$**
	Daisy	**-3.36$_3$**		-1.55	**4.07$_3$**	0.96	**-3.04$_2$**	**-4.12$_3$**	**3.75$_3$**
	Yoda*	**6.90$_3$**	**-4.18$_3$**		**2.69$_2$**	**-5.98$_3$**	**2.87$_2$**	**5.81$_3$**	**-4.14$_3$**
	Zoe	**-1.98$_1$**	**2.54$_1$**	-0.91		1.88	0.88	**-2.42$_1$**	**-2.19$_1$**
	Lilly#	-0.94	-1.66	-0.43	**2.26$_1$**		**3.01$_2$**	-1.15	-1.04
	Claudette	-1.13	**-1.99$_1$**	-0.52	**-1.97$_1$**	**5.24$_3$**		-1.39	0.57
	Amber	-1.27	0.46	-1.08	**-4.09$_3$**	**6.50$_3$**	**-2.12$_1$**		-1.12
	Joyce	-1.31	**6.83$_3$**	-0.60	**-2.29$_1$**	**-2.54$_1$**	0.71	-1.61	

Table 3. Index of affiliation results for specific chimpanzee pair associations following merging of two groups at the Johannesburg Zoo, South Africa. Dark grey cells represent increases in association following merging while light grey cells represent decreases in association following merging. Individuals are listed in order of decreasing age with the dominant male highlighted with a star (*) and dominant female highlighted with a hash (#)

		Directed at:							
		Thabu	**Daisy**	**Yoda***	**Zoe**	**Lilly#**	**Claudette**	**Amber**	**Joyce**
Received by:	**Thabu**		0.10	-0.38	0.00	0.00	0.05	-0.05	0.29
	Daisy	0.14		0.21	-0.26	-0.28	0.00	0.12	0.06
	Yoda*	-0.81	0.00		0.52	0.07	0.09	0.14	0.00
	Zoe	0.00	-0.68	0.14		0.54	0.00	0.00	0.00
	Lilly#	0.25	-0.70	0.13	-0.17		0.49	0.00	0.00
	Claudette	0.00	0.00	0.41	0.18	0.32		0.00	0.09
	Amber	0.02	0.16	0.44	0.00	0.36	0.00		0.02
	Joyce	0.00	-0.60	0.00	0.00	0.00	-0.40	1.00	

Prior to her removal, Claudette received the highest number of interactions of all adults within the group, surpassed only by the interactions of the two juveniles, Joyce and Charles. Claudette's interactions were initiated by Yoda (77%), Amber (18%) and Charles (5%).

The removal of Claudette was associated with various changes in directed and received association as well (Table 5). As with the merging manipulation in experiment 1, overall patterns suggest a mixed response of selective increasing and decreasing of associations between individuals, with no clear patterns for any particular age/sex/dominance class. The greatest decrease in association involving males was in interactions by Charles (juvenile male) directed at his sister, Joyce. Amongst females, Lilly (dominant female) displayed the greatest reduction in her interactions directed at Yoda (dominant male). Among the males, the greatest increase in association was in interactions directed at Yoda by Thabu. Among females, Daisy displayed the greatest increase in interactions, directed at her son Amber.

Table 4. Z statistics for a χ^2 using adjusted residuals used to examine specific chimpanzee pair associations at the Johannesburg Zoo, South Africa, before and after the removal of an adult female (Claudette). Bold Z values in grey cells denote significant interactions and subscripts denote level of significance ($_3 p < 0.001$; $_2 p < 0.01$; $_1 p < 0.05$). Individuals are listed in order of decreasing age with the dominant male highlighted with a star (*) and dominant female highlighted with a hash (#)

		Claudette Present							
		Thabu	**Daisy**	**Yoda***	**Zoe**	**Lilly#**	**Amber**	**Joyce**	**Charles**
Claudette Absent	**Thabu**		**-2.73$_2$**	0.46	**-5.08$_3$**	1.52	**20.34$_3$**	**-2.82$_2$**	**-5.89$_3$**
	Daisy	**-2.57$_1$**		**-2.88$_2$**	**-3.42$_3$**	-1.70	**-2.71$_2$**	**9.84$_3$**	**2.74$_2$**
	Yoda*	**13.92$_3$**	**-9.01$_3$**		**9.64$_3$**	**5.91$_3$**	**-5.32$_3$**	**-4.02$_3$**	**-2.25$_1$**
	Zoe	**-2.67$_2$**	**13.54$_3$**	**-3.37$_3$**		-1.76	**-4.12$_3$**	**-3.35$_3$**	**-5.06$_3$**
	Lilly#	-1.01	**-2.75$_2$**	**10.69$_3$**	-0.64		0.61	-1.27	**-2.15$_1$**
	Amber	-1.78	**6.40$_3$**	**-2.24$_1$**	**-4.01$_3$**	-1.17		0.83	-0.74
	Joyce	**-3.31$_3$**	**4.66$_3$**	**-4.19$_3$**	**-7.29$_3$**	**-2.19$_1$**	**-4.59$_3$**		**9.98$_3$**
	Charles	**-4.25$_3$**	**-6.56$_3$**	**5.53$_3$**	**5.59$_3$**	-1.15	0.36	0.73	

Table 5. Index of affiliation results for specific chimpanzee pair associations following removal of an adult female (Claudette) at the Johannesburg Zoo, South Africa. Dark grey cells represent increases in association following removal of the female while light grey cells represent decreases in association following removal. Individuals are listed in order of decreasing age with the dominant male highlighted with a star (*) and dominant female highlighted with a hash (#)

		Directed at:							
		Thabu	**Daisy**	**Yoda***	**Zoe**	**Lilly#**	**Amber**	**Joyce**	**Charles**
Received by:	**Thabu**		0.00	0.62	0.00	0.00	0.24	0.00	0.14
	Daisy	0.08		0.01	0.04	0.00	0.20	-0.13	-0.19
	Yoda*	-0.19	-0.03		0.59	-0.19	0.00	0.00	-0.17
	Zoe	0.00	0.05	0.05		-0.17	0.00	0.01	0.06
	Lilly#	1.00	0.00	-1.00	0.00		0.00	0.00	0.00
	Amber	0.00	0.00	0.00	0.00	-0.05		-0.04	0.09
	Joyce	0.00	0.04	0.17	0.00	0.00	0.09		-0.31
	Charles	0.01	-0.17	-0.12	0.21	0.05	0.31	-0.29	

Discussion

This study aimed to examine the behavioural responses of captive chimpanzees to social changes similar to those seen in nature. The first experiment investigated the merging of two distinct groups into a single multi-male, multi-female group and the second experiment investigated the impact that the removal of an individual female had on the behaviour of a captive chimpanzee group. Both manipulations were associated with an increase in the levels of social grooming, supporting my prediction that social change would

be associated with increased affiliative interactions. Contrary to my prediction that social change would be associated with increased agonistic behaviour, neither manipulation generated any increases in aggression. The Group Merging treatments generated an overall decrease in aggression, while the Individual Removal study generated no change in aggression. However, aggression levels were generally low in all treatments. Only one of the two experiments (Group Merging) was associated with changes in stress-related behaviour in the form of increased abnormal behaviour and self-directed grooming following merging.

Both the Group Merging and Individual Removal experiments were associated with significantly increased scores for 'Hidden'. This result should be interpreted with caution as it may reflect an active decrease in the time spent by the chimpanzees in view of the public, or the behaviour scoring of the observer due to my visual inaccessibility in parts of the enclosure. The latter obviously has little relevance when interpreting the behaviour of the chimpanzee group(s) whereas the former might suggest increased stress as proximity to humans may be a great source of stress (Morgan & Tromborg, 2007). To clarify, other stress-related behaviours should be examined in conjunction with this result, as set out below.

The merging of the groups was also associated with an increase in abnormal and self-directed behaviour, in the form of self-grooming. Many abnormal behaviours appear to be stress-related (Baker & Easley, 1996; Tiefenbacher *et al.*, 2004), functioning as a means to 'discharge' stress (Fox, 1984) and primates in particular also exhibit increased self-directed behaviour, such as self-scratching and self-grooming (Aureli & de Waal, 1997; Carder & Semple, 2008), in response to stress. Many studies have interpreted such behavioural changes as being indicative of changes in the experience of stress (Clarke *et al.*, 1982; Cordoni & Palagi, 2007) and in the present study, the increased abnormal and self-directed behaviour suggest that the chimpanzees experienced the merging of the groups as a stressful event.

Interestingly, the Individual Removal treatments generated no increases in abnormal or self-directed behaviour, suggesting that the removal of Claudette was not as stressful as the merging of the groups. The increased levels of public interaction followed Claudette's removal, compared to the lack of significant change in levels of 'Other' behaviours in Group Merging (public interactions were included in the 'Other' category), also suggest that the Individual Removal treatments were not as stressful as the Group Merging treatments. Close proximity to and interaction with zoo visitors is considered to indicate a relatively relaxed state amongst primates (Chamove *et al.*, 1988; Wells, 2005).

While the removal of Claudette did not appear to generate any overt changes in stress-related behaviour, the removal of Claudette, as well as the Group Merging, generated various

shifts in the social interactions of the chimpanzee group, suggesting that the group social structure was altered. Instability in the social hierarchy can be a source of stress for individuals (Setchell *et al.*, 2010) and chimpanzees appear to respond to social uncertainty through specific affiliative interactions (Okamoto *et al.*, 2001; Watts, 2006). Under potentially volatile social conditions, chimpanzees can either attempt to cement existing social relationships, thereby stabilising the social environment (Lemasson *et al.*, 2005; Koyama *et al.*, 2006), or increase affiliation with dominants to reduce the likelihood of being the target of their aggression (Vessey, 1971; Nakamichi *et al.*, 1995).

However, my data offer little clarification as to the causality of the changes in the associations among individuals in the study population. Because both individuals increased their interactions with one another, the interactions of Lilly (dominant) and Claudette (low rank) in the Group Merging treatments suggest an attempt to reinforce an existing bond while the Zoe: Lilly associations suggest an attempt by Zoe (low rank) to placate Lilly as Lilly decreased her interactions directed at Zoe, but Zoe increased her interactions directed at Lilly. The interactions of Amber (low rank) and Yoda (dominant) appear to contradict both of these suggestions as the Amber: Yoda association, initially highly significant, became non-significant following the group merger, but this could be the result of increased available social partners.

The changing associations in the Individual Removal results show a similarly unclear pattern. Both before and after the removal of Claudette, Lilly and Yoda were highly associated, suggesting an attempt to cement an existing relationship. Similarly, Daisy: Joyce maintained a significant positive association. The Thabu: Yoda association, originally not significant, became a significant positive association following the removal of Claudette, suggesting that Thabu may have been attempting to placate dominant Yoda. In both experiments, the patterns appear to conform to the relationship reinforcement (Lemasson *et al.*, 2005; Koyama *et al.*, 2006) and placation (Vessey, 1971; Nakamichi *et al.*, 1995) tactics described in the literature.

The observed patterns of changes in association in response to social disruption may not be predictable and may be individually context specific, based both on existing inter-individual relationships and the type of disturbance experienced. Chimpanzees are well documented to exhibit context-specific behavioural responses to a variety of social challenges (crowding: Aureli & de Waal, 1997; competitive VS cooperative tasks: Hare & Tomasello, 2004) and also appear to display sex-specific responses to the reintroduction of familiar individuals (Okamoto *et al.*, 2001).

One unusual outcome in these experiments was the lack of change in levels of aggression in the Individual Removal and the slight decrease in aggression in the Group Merging experiments. Previous primate studies have suggested that social disruption is associated with increasing aggression (captive Rhesus monkeys: Southwick, 1967; free-ranging Rhesus monkeys: Vessey, 1971; Squirrel monkeys: Williams & Abee, 1988; Chimpanzees: Baker *et al.*, 2000; Campbell's monkeys: Lemasson *et al.*, 2005). However, chimpanzees appear to be sensitive to levels of social tension and moderate social tension through increased affiliative interactions as illustrated by the findings of Okamoto *et al.* (2001) whereby the reintroduction of chimpanzees following separation was associated with no change in aggression and increased affiliative interactions. The lack of change in aggression as well as the increased social grooming in this study agrees with the findings of Okamoto *et al.* (2001). Thus, chimpanzees may suppress aggression during such encounters or utilize submissive greeting to diffuse aggression immediately (Nieuwenhuijsen & de Waal, 1982) in much the same manner as they respond to spatial restriction (de Waal, 1989). Overt aggression is rare in natural chimpanzee communities (Wallace, 1979) but the degree to which this explains the observed patterns of behaviour in my study requires further investigation. Individual familiarity in this study and that of Okamoto *et al*. (2001) may also confound interpretations of these results as chimpanzees may retain knowledge of previous social interactions between individuals (Aureli *et al.*, 2008).

In addition to offering new insights into chimpanzee socio-dynamics, my study has important implications for animal welfare. Social isolation, instability and unnatural groupings are well known to be stressful for captive animals (Morgan & Tromborg, 2007) and some authors have suggested that such social interventions should be discouraged (Olsson & Westlund, 2007) or avoided outright (Baker *et al.*, 2000). Chimpanzees are thought to cope better with social than structural environmental change (Reimers *et al.*, 2007) and the outcomes of my study in conjunction with those of Okamoto *et al*. (2001) suggest that perhaps the risks associated with social change in chimpanzees are not as severe as for other species. Not only is this of importance for routine husbandry and socialisation, but may also be of particular importance for inter-institutional breeding programs which often require the exchange and integration of unrelated and unfamiliar individuals between existing groups.

In conclusion, both experiments generated similar effects whereby the chimpanzees exhibited increased affiliative behaviour and stable or decreased agonistic behaviour in response to social change. Both changes in the social conditions appear to have generated varying degrees of social change and subsequent stress for the chimpanzees. The degree of

stress experienced appears to have been dependent on the nature of the manipulation with the Group Merging being comparatively more stressful than the Individual Removal, as evidenced by an increase in self-directed grooming and abnormal behaviours. The degree to which the behaviour of the chimpanzees mirrors that of free-ranging populations remains to be tested. My study is the first to examine these types of social change in captive chimpanzees. Both social manipulations investigated in this study also potentially mirror social disruptions that chimpanzees might experience in nature (merging following party formation and individual emigration), changes which have received little or no investigation in the existing primate literature. Future studies should focus on natural populations and examine the effects of such social changes in these contexts.

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Appendices: Tables of chimpanzee associations

Appendix 1. Raw data for total counts of inter-individual interactions, regardless of which individual directed or received the interaction, for two groups of captive chimpanzees at the Johannesburg Zoo, South Africa, before and after merging of the two groups. The dominant male is indicated by a star (*) and the dominant female is indicated by a hash (#)

		Total Associations when Separated							
		Thabu	**Daisy**	**Yoda***	**Zoe**	**Lilly#**	**Claudette**	**Amber**	**Joyce**
Total Associations when Merged	**Thabu**		0	5	0	0	0	1	0
	Daisy	10		0	34	29	0	0	19
	Yoda*	26	9		0	0	0	0	0
	Zoe	0	15	34		4	0	0	0
	Lilly#	0	0	5	15		3	0	0
	Claudette	2	0	14	4	12		0	2
	Amber	9	13	30	0	18	0		0
	Joyce	12	16	0	0	0	2	5	

Appendix 2. Raw data for total counts of directed and received inter-individual interactions for two groups of captive chimpanzees at the Johannesburg Zoo, South Africa, before and after merging of the two groups. The dominant male is indicated by a star (*) and the dominant female is indicated by a hash (#)

			Directed at:							
			Thabu	**Daisy**	**Yoda***	**Zoe**	**Lilly#**	**Claudette**	**Amber**	**Joyce**
Received By:	*Separated Treatment*	**Thabu**		0	3	0	0	0	1	0
		Daisy	0		0	20	14	0	0	16
		Yoda*	2	0		0	0	0	0	0
		Zoe	0	14	0		0	0	0	0
		Lilly#	0	16	0	4		3	0	0
		Claudette	0	0	0	0	0		0	0
		Amber	0	0	0	0	0	0		0
		Joyce	0	3	0	0	0	2	0	
	Merged Treatment	**Thabu**		4	15	0	0	2	8	12
		Daisy	6		9	6	0	0	5	16
		Yoda*	11	0		30	4	5	8	0
		Zoe	0	9	4		15	0	0	0
		Lilly#	2	0	1	0		5	0	0
		Claudette	0	0	9	4	7		0	2
		Amber	1	8	22	0	18	0		1
		Joyce	0	0	0	0	0	0	4	

Appendix 3. Raw data for total counts of inter-individual interactions, regardless of which individual directed or received the interaction, for a group of captive chimpanzees at the Johannesburg Zoo, South Africa, before and after the removal of an adult female (Claudette). The dominant male is indicated by a star (*) and the dominant female is indicated by a hash (#)

		Total Associations with Claudette Present							
		Thabu	**Daisy**	**Yoda***	**Zoe**	**Lilly#**	**Amber**	**Joyce**	**Charles**
Total Associations with Claudette Absent	**Thabu**		0	7	0	0	0	0	0
	Daisy	14		1	10	0	0	35	43
	Yoda*	48	2		0	14	0	0	38
	Zoe	0	99	78		2	0	0	9
	Lilly#	1	0	10	0		3	0	0
	Amber	19	37	0	0	3		2	13
	Joyce	0	76	4	1	0	4		97
	Charles	12	39	44	96	4	36	25	

Appendix 4. Raw data for total counts of directed and received inter-individual interactions for a group of captive chimpanzees at the Johannesburg Zoo, South Africa, before and after the removal of an adult female (Claudette). The dominant male is indicated by a star (*) and the dominant female is indicated by a hash (#)

			Directed at:							
			Thabu	**Daisy**	**Yoda***	**Zoe**	**Lilly#**	**Amber**	**Joyce**	**Charles**
Received By:	*Claudette Present Treatment*	**Thabu**		0	0	0	0	0	0	0
		Daisy	0		0	5	0	0	25	18
		Yoda*	7	1		0	10	0	0	18
		Zoe	0	5	0		2	0	0	5
		Lilly#	0	0	4	0		0	0	0
		Amber	0	0	0	0	3		2	2
		Joyce	0	10	0	0	0	0		48
		Charles	0	25	20	4	0	11	49	
	Claudette Absent Treatment	**Thabu**		0	48	0	0	19	0	11
		Daisy	14		2	26	0	37	71	34
		Yoda*	0	0		70	10	0	0	39
		Zoe	0	73	8		0	0	1	76
		Lilly#	1	0	0	0		0	0	0
		Amber	0	0	0	0	3		2	3
		Joyce	0	5	4	0	0	2		12
		Charles	1	5	5	20	4	33	13	

Chapter 5. Shade as a thermoregulatory resource for captive chimpanzees

Abstract

Under natural conditions, animals employ a variety of thermoregulatory tactics and primates, in particular, exhibit extensive flexibility in thermoregulatory behaviour. In contrast, captive environments may impose restrictions on the expression of behavioural thermoregulation. Thus, my study aimed to examine the utilization of shade by a group of captive chimpanzees as a means of thermoregulation. I recorded behaviour and location within the enclosure of a group of captive chimpanzees, simultaneously noting shade and sun utilization. Shade was utilized significantly more often than areas with direct sun, particularly during the hotter midday than the cooler mornings. The chimpanzees also appear to utilize shade both when shade availability is limited and abundant. These findings suggest that shade constitutes a valuable environmental resource for captive primates.

Introduction

Animals are often subject to variation in environmental temperature and respond through thermoregulatory mechanisms. Thermoregulation balances heat gain/production with heat losses to the surrounding environment (Castellini, 2009) in an attempt to maintain thermal neutrality (Dahl & Smith, 1985), and is under the control of the preoptic and anterior hypothalamus (Gale *et al.*, 1970; Laudenslager, 1976). The thermal environment can exert a strong influence on behaviour (Dahl & Smith, 1985; Hill *et al.*, 2004) and particular behavioural traits, such as cathemerality, may have evolved in response to thermal stressors (Hill, 2006b).

Thermoregulation can occur through either autonomic/physiological or behavioural mechanisms (Jaehne *et al.*, 2005). In mammals, the primary physiological mechanism for shedding excess heat is via evaporative cooling, which can only account for 20-30% of heat loss (Langman *et al.*, 1996). Behavioural thermoregulation, by contrast, offers an effective means of controlling body temperature while minimizing water loss and maximizing time allocated to activities such as feeding (Barton *et al.*, 1992).

In a given environment, animals may choose to remain in that environment and thermoregulate through physiological or behavioural means, or may simply avoid that environment through modified activity patterns and microhabitat selection (Stelzner & Hausfater, 1986). Such thermoregulatory decisions are governed by the perceptions of individuals of their environment, based on factors such as ambient temperature, solar radiation, humidity and wind speed and direction (Hill *et al.*, 2004), and the relative costs and benefits of the behaviour. For example, instead of actively seeking out and resting in the shade, Yellow baboons *Papio cynocephalus* make fewer directed movements and travel more slowly in areas of high shade than direct sun (Stelzner, 1988). Both behaviour patterns are forms of behavioural thermoregulation but the former may place baboons at greater risk of predation or reduced foraging efficiency (Stelzner, 1988).

Primates occupy a variety of habitats ranging from high-altitude montane environments (Iwamoto & Dunbar, 1983) to tropical rainforests (Lehmann *et al.*, 2010), each with its own thermoregulatory challenges. Primates exhibit extensive behavioural flexibility (Olsson & Westlund, 2007) and employ a variety of behavioural strategies for thermoregulation (Kosheleff & Anderson, 2009). For example, under cold conditions, Japanese macaques *Macaca fuscata* engage in hot spring bathing as a means of conserving heat (Zhang *et al.*, 2007) while long-tailed macaques *Macaca fascicularis* appear to increase affiliation and decrease social spacing (Schino & Troisi, 1990). Furthermore, Gelada baboons *Theropithicus gelada* increase active foraging to ensure sufficient energy for heat production (Iwamoto & Dunbar, 1983) while Yellow baboons alter posture and orientation to minimize heat loss during periods of low temperature (Stelzner & Hausfater, 1986).

In response to the high ambient daytime temperatures and intense solar radiation of open equatorial (Wheeler, 1994) and savanna habitats (Hill *et al.*, 2004), Chacma baboons *Papio ursinus* reduce activity (Hill, 2006b) and increase shade seeking (Hill, 2006a), such as using caves (Barret et al., 2004). In contrast to open equatorial habitats, equatorial rainforest environments provide cover, limiting solar radiation (Hiley, 1976). Rainforests are unusual because solar radiation heats up the canopy and not the ground (Takemoto, 2004), effectively creating a light and temperature gradient from treetop to ground level (Théry, 2001; Takemoto, 2004). In response, chimpanzees *Pan troglodytes* utilize these gradients by actively moving from ground to canopy according to their thermal needs (Takemoto, 2004). Like baboons, chimpanzees occasionally utilize cave microclimates as thermal refugia (Pruetz, 2007) and actively regulate exposure to direct sunlight (Kosheleff & Anderson, 2009).

Most non-human primates inhabit tropical climes, but, under captive conditions, are often housed in climates different to their natural settings (Coe, 1989; Lindburg, 1998). Yet, little research has investigated the effects of the thermal environments on captive primate wellbeing (Lindburg, 1998) despite the associated stress (Mitlöhner *et al.*, 2002) and mortality (Brockman *et al.*, 1987). Furthermore, most research into the effects of the thermal environment on captive primates has examined physiological thermoregulation (Benedict & Bruhn, 1936; Morrison, 1962; Whitford, 1976) with only a few direct examinations of behavioural thermoregulation (Dahl & Smith, 1985; Troisi & Schino, 1987; Schino & Troisi, 1998).

Most information on captive animal thermoregulation draws from agriculture due to the direct impact on productivity (Ray & Roubicek, 1971), which has highlighted the importance of shade for animal wellbeing (Ray & Roubicek, 1971; Schütz *et al.*, 2008; Tucker *et al.*, 2008). Studies of free-ranging species have demonstrated the inherent value of variable microhabitats for thermoregulation (Young, 1982) and studies of non-agricultural captive species have reached similar conclusions regarding the importance of shade (Langman *et al.*, 1996; Langman *et al.*, 2003).

A number of studies of space use and environmental complexity have suggested that the tendency of apes to spend time around buildings (Ogden *et al.*, 1990) may be related to thermoregulatory benefits of the microclimates around these structures (Stoinski *et al.*, 2001a; Stoinski *et al.*, 2001b), suggesting the importance of considering the thermal needs of an animal when planning captive environments. It is commonly held that shade panels (Bohm Jr *et al.*, 2009) and climbing structures and platforms are important as they create diverse microclimates within enclosures (Swaisgood & Shepherdson, 2005). Furthermore, naturalistic enclosure designs have become common practice for most captive institutions (Fàbregas *et al.*, 2011) but whether they provide the animals with all the necessary elements for biological functioning, such as shade, remains to be tested.

The aim of this study is to investigate the behavioural thermoregulation of a group of captive chimpanzees at the Johannesburg Zoo, South Africa, with regard to shade utilization within their naturalistic outdoor enclosure. The enclosure at the Johannesburg Zoo comprises a variety of trees and walls which generate a spatially and temporally dynamic thermal environment. My study was conducted over the austral winter/spring, during which the mean daily temperature was approximately 13.7˚C (mean daily minimum and maximum temperatures over the study period were 6.1˚C and 21.3˚C respectively). The chimpanzee thermal neutral zone (TNZ) appears to lie between 17˚C and 29˚C (Benedict & Bruhn, 1936)

and mean core body temperature for chimpanzees is 37.25˚C (Morrison, 1962). Chimpanzees in equatorial grassland and rainforest environments experience mean daytime temperatures of between 24.6 - 29.6˚C, with daily maximum temperatures of between 37 - 42˚C, depending on the habitat type (Pruetz, 2007). Therefore, my first prediction is that the chimpanzees would utilize direct sun more than shade, as the climate at the Johannesburg Zoo is substantially cooler than the natural equatorial range of chimpanzees and thus is likely to be below or just within the lower limits of the chimpanzee TNZ.

The second prediction is that high daily maximum and low daily minimum temperatures would be associated with greater and lesser shade utilization respectively. I also predicted that shade and sun utilization would vary according to the time of day, with shade being utilized less during the cooler morning and afternoon periods than at midday.
The third prediction is that inactivity would occur more in shade than in sun. Inactivity is typically associated with energy conservation in hotter conditions (Kosheleff & Anderson, 2009) and high heat load (Hill *et al.*, 2004) and resting in shade reduces environmental heat gain through solar radiation and endogenous heat production (Wheeler, 1994).

Materials and Methods

Study subjects

This study was carried out from May 2008 to September 2008, during the austral winter/spring. The subjects were a socially housed group of captive chimpanzees at the Ape House at the Johannesburg Zoo, South Africa. The group comprised four males (Thabu: 24 years; Yoda: 16 years; Amber: 9 years; Charles: 1 year) and five females (Daisy: 24 years; Zoe: 13 years; Lilly: 16 years; Claudette: 12 years; Joyce: 5 years). The group had been together for approximately four years but had experienced a social disturbance in the form of a four month separation into two groups; the study took place two months after the group was reunited.

Housing and husbandry

The chimpanzees were housed in a large indoor-outdoor exhibit at the Johannesburg Zoo Ape House, with the outdoor section providing an approximate total area of 2 500m^2 (Figure 1). The outdoor area was divided into two sections (Section 1: 1 000m^2; Section 2:

1 500m^2) by an 8m wall, capped with electric fencing, with an interconnecting doorway, allowing the chimpanzees free movement between both sections. The enclosures were surrounded by similar 8m walls on all sides apart from those areas bordered by moats (approximately 4-5m wide), with rear walls providing access-doors to the night rooms, each with a lowered concrete ramp leading to the door. Section 1 also had a series of large reinforced-glass viewing windows incorporated into a section of the wall. Moats were bordered with 1.5m high electric fencing; 30cm high electric fencing also extended out of the water approximately 2m from the edge of the enclosure.

Each enclosure section differed in structure and composition and included a variety of trees, shrubs, rocks and felled trees; the placement, size and type varied between sections (Figure 1). Section 1 comprised six trees (3-5m high), a few small felled trees and a number of rocks throughout. Section 2 provided two living trees (2-4m high) and two large felled trees for climbing. There was also an embankment of rocks, a stream connecting two sections of moat and a pair of concrete artificial termite mounds located in section 2. In both sections, the surrounding walls provided variable shade throughout the day with trees outside the enclosure also providing a degree of shade, particularly in section 1 where trees were very large (approximately 10-15m high). However, the trees were mostly deciduous and had few leaves during the study period.

The chimpanzees were fed a variety of fresh fruit and vegetables, primate pellets and boiled egg twice daily. Food was scattered randomly throughout the outdoor enclosures in the morning to encourage the chimpanzees to leave their night-rooms. Similarly, food was scattered randomly throughout the night-rooms in the evenings to encourage the chimpanzees to re-enter the night-rooms. The chimpanzees had full access to both outdoor sections of their enclosure from 10h00 to 15h00 on weekdays and from 10h00 to 16h00 on weekends. The night rooms were unheated.

Behavioural observation

Behaviour was recorded according to the categories described in Table 1 using an instantaneous focal animal sampling technique with a 1 minute inter-sample interval (Martin & Bateson, 1986). Observation sessions were carried out over a period of 10 non-consecutive days for each individual chimpanzee sampled over the full study period (May – September 2008). Sessions commenced on the hour, lasting 60 minutes, between 10h00 and 15h00, covering the full 5 hours that the chimpanzees were in their outdoor enclosures.

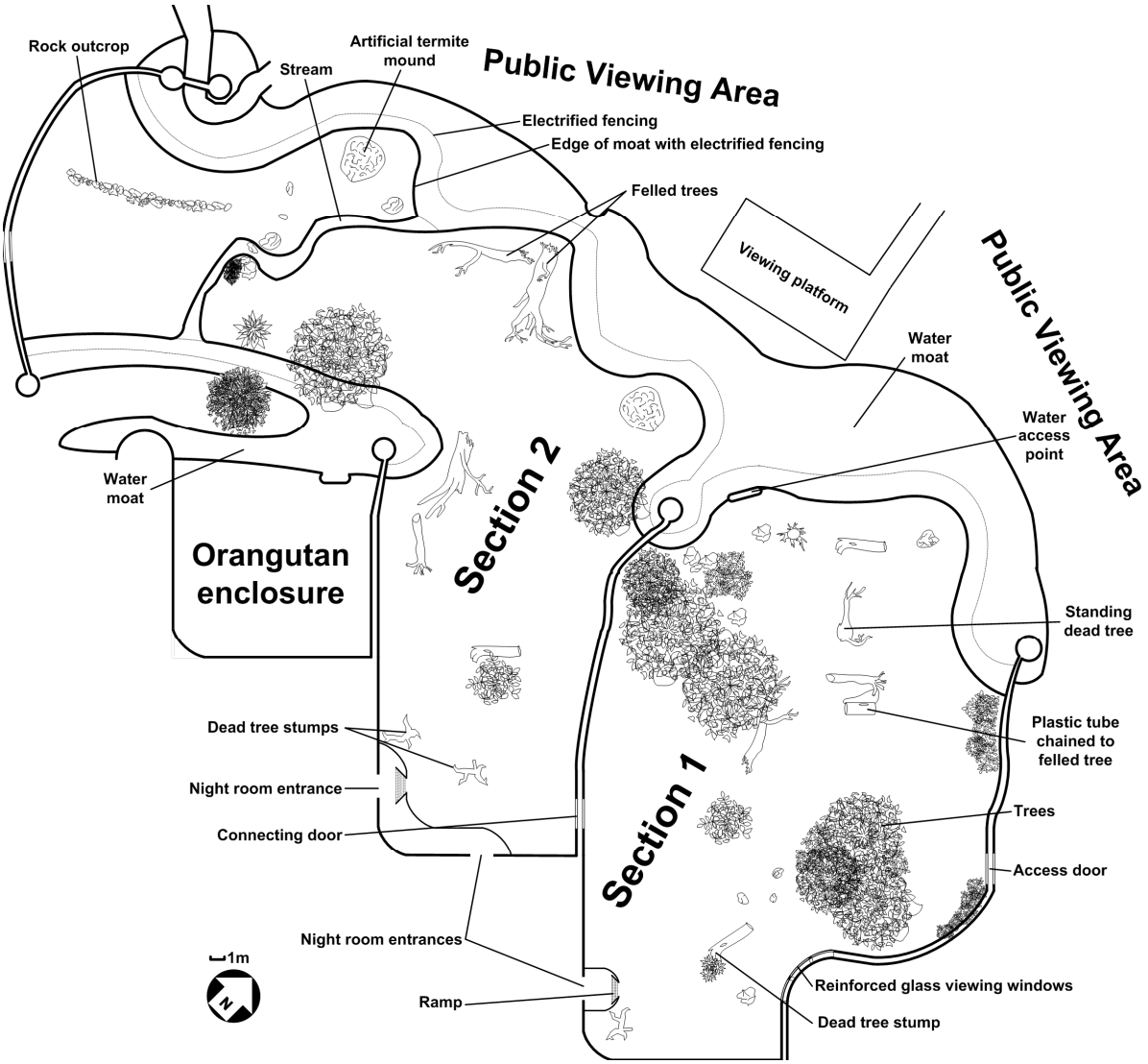

Figure 1. Outdoor housing area of the chimpanzee exhibit at the Johannesburg Zoo Ape House, South Africa, drawn to scale.

All individuals, with the exception of two, were sampled, resulting in a total of 10 hours of observation per individual for 8 individuals. At the time of the study Claudette was planned to be removed from the group (see Chapter 4), but the timing of her removal was unconfirmed and thus she was not included in observations. However, her removal occurred approximately two weeks after completion of observations for this study. Charles was also excluded, on the basis that he was very young and still engaged in ventral-ventral contact with his mother and thereby relatively immobile.

For all behaviour, whether or not the focal individual was in the shade was recorded. Individuals were considered to be in the sun when their head or any part of their trunk was in direct sun. In addition, I divided the enclosure into eight zones (Figure 2). Zones were

defined based on their general patterns of shade distribution such that certain zones, such as A and F, provided almost no shade, lacking environmental features that generated shade. Other zones, such as zones C and D were heavily shaded by vegetation in the enclosure or just outside the enclosure. The zone that the focal individual occupied at each sample time was also recorded. Therefore, for each individual, I recorded its behaviour (Table 1), whether it was in the sun or shade and what zone it occupied (Figure 2). At the start of each observation session, the level of available shade was estimated visually and recorded as a percentage of the total surface area for each specific zone.

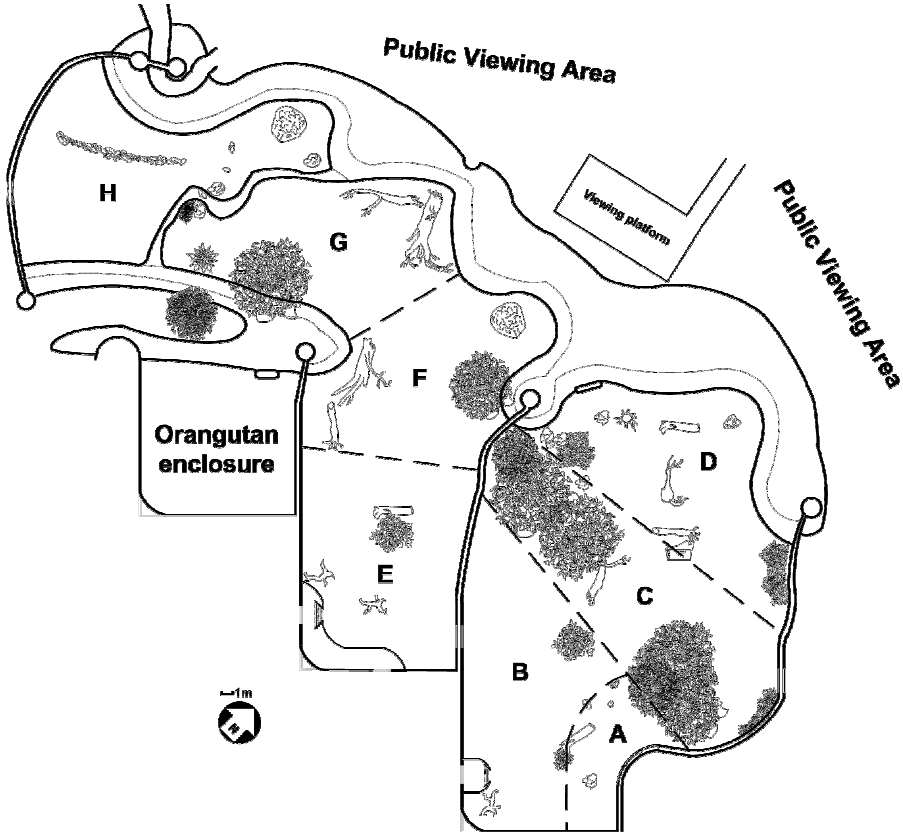

Figure 2. Outdoor housing area of the chimpanzee exhibit at the Johannesburg Zoo Ape House, South Africa, drawn to scale. Dashed lines denote zonation (zones A-H labelled with uppercase bold letters) of the enclosure based on variable shade patterns.

Data analysis

For overcast days, all behaviour, shade and location data were excluded from further analysis so as not to bias results toward greater shade use. This resulted in the exclusion of 9 hours, and a final dataset comprising 61 hours. Prior to analysis, behaviour categories were combined into four broad categories. 'Active' behaviour included travel, foraging, object play

and locomotor play, 'Inactive' behaviour included vigilance, inactivity, abnormal behaviour (abnormal gait was not observed and thus all observed abnormal behaviour could be considered as inactive behaviour) and self-directed grooming while 'Social' behaviour included aggression, social play and social grooming. Any recorded behaviour that did not fit into these categories were now placed within the 'Other' behaviour category.

Observation sessions were classified according to their start time, such that a session starting at 11h00 and ending at 12h00 was classified as '11h00'. The number of hours of data collected in each time slot were: 10h00 – 14hrs; 11h00 – 14hrs; 12h00 – 11hrs; 13h00 – 14hrs; 14h00 – 8hrs. Hours in each time slot were balanced for all individuals except time slot 12h00, for which Thabu, Zoe and Joyce were excluded due to overcast days, and time slot 14h00, for which Thabu, Daisy, Lilly, Yoda, Amber and Joyce were excluded due to overcast days. The enclosure zones were classified according to their levels of shade at the start of each session, and categorised into tertiles of 0-30% shade designated as 'low' shade zones, 31-69% as 'medium' shade zones and 70-100% as 'high' shade zones.

To investigate the potential effects of weather conditions on shade utilization, data from the nearest weather station were obtained through the South African Weather Service. Maximum and minimum temperature data, measured to the nearest degree centigrade, were collected for the appropriate sampling days. Humidity is likely to fluctuate sporadically across the day and with the movement of air (Dahl & Smith, 1985) and appears to play little role in both captive (Schino & Troisi, 1990) and free-ranging primate thermoregulation (Barrett *et al.*, 2004). For these reasons, humidity was not considered. While wind speed and direction are likely to influence an individual's perceived environmental temperature (Hill *et al.*, 2004), prevailing wind conditions were not considered because the 8m high walls surrounding the outdoor enclosure possibly restricted air movement.

All analyses were two-tailed with a model significance level of $p = 0.05$ and were conducted using R (Ver. 2.13.0; R Development Core Team, 2011). First, a Pearson's χ^2 test was used to assess whether there were any differences in overall shade/sun utilization patterns based on scores for total behaviour in the sun and total behaviour in shade, regardless of behaviour type. These totals were compared to an even sun/shade distribution. The levels of sun and shade utilization were significantly different ($\chi^2_1 = 352.595$; $p < 0.001$), suggesting that shade was utilized at levels higher than expected by chance while sun areas were utilized at levels lower than expected by chance.

Table 1. Definitions of behaviour observed in the chimpanzee groups at the Johannesburg Zoo, South Africa, to assess the influence of shade availability on space utilization and behaviour

Behaviour	***Definition***
Travelling	Movement from one location to another, not obviously searching for food. Included walking, running and climbing
Foraging	Searching for, manipulating or consuming food or drink.
Vigilance	When the animals ceased other activities in order to monitor or observe their surroundings or other individuals
Inactive	Resting, either standing, sitting or lying down. Included sleeping
Abnormal	Coprophagia/urophagia, self-mutilation, faeces throwing and hair plucking. Other behaviour was scored as abnormal based on the context in which they occurred and whether they occurred repetitively (>3 times in succession; Jones *et al.*, 2008). These included nipple pulling, abnormal gait and posturing and chronic masturbation
Aggression	Chasing aggressively (characterised by sneering, open and closed grins and compressed lip faces. Usually associated with screams, barks and 'wraaa' calls; Goodall, 1986) or fighting with one another. Included aggressive gesturing or signalling
Social play	Wrestling, playful biting and playful chasing (characterised by a relaxed face, possibly with a drooping lower lip, or a full play face. Usually silent but may include soft grunts or hoots; Goodall, 1986)
Object play	Play directed at or involving an inanimate object
Locomotor play	Solitary active play. Included running, rolling, swinging or somersaulting
Self-grooming	Licking, cleaning, picking at and removing items from their own skin or hair. Included self-scratching
Being groomed	When individuals made no effort to engage in other activities in order to be licked, cleaned or have items from the skin or hair removed by others
Grooming others	Licking, cleaning and removing items from the skin or hair of others
Other	Any identifiable behaviour that did not obviously fit into the other behaviour categories
Hidden	Chimpanzees were obscured from view or behaviour was unidentifiable according to the other categories listed

Based on the results of the χ^2 test, further analyses were conducted to investigate the influences of behaviour and the thermal environment on the utilization of shade. All further analyses used a generalized linear model, involving a binomial error structure and a logit link function. Combined response variables were created using the *cbind* function in the *stats* package in R, which takes into account the number of values (in this case, number of observations in the sun or shade for example) making up the ratio of the response and is an appropriate method for non-normal error structure and non-constant variance (Crawley, 2007). Due to the low sample size, behaviour and the thermal environment were investigated

separately and any interactions between behaviour and other factors were only examined graphically. A generalized linear model (GLZ), using the *glm* function in the *stats* package (R Development Core Team, 2011), was used to investigate whether particular behaviours were associated with shade and/or sun utilization. Behaviour category was used as the categorical predictor while counts of each behaviour in the sun and shade respectively were used as a combined response variable.

Another GLZ analysis was used to assess the availability of shade over time, again using the *glm* function. Time of day was used as a categorical predictor while the number of 'Low' and 'High' shade tertile zones only (i.e. 'Medium' tertile zones were excluded) were used as a combined response variable, as these represent the zone conditions in which thermoregulatory decisions are likely to be most definitive and to avoid bias in tertile boundaries (e.g. between 30 and 31% which distinguished low and medium tertiles).

A generalized linear mixed-effects model (GLMZ), using *lmer* function in the *lme4* package (Bates *et al.*, 2011) was used to investigate how shade utilization might vary with location in the enclosure, available shade, ambient weather conditions and time of day. Time of day and shade tertile were used as categorical predictors while the counts of individuals being in the sun and shade were used as a combined response variable. Within the shade tertile variable, only 'High' and 'Low' tertiles were examined. Daily maximum and minimum temperatures were included as covariates. In addition, chimpanzee identity, to account for repeated measures of the same individuals, and the zone occupied, as the enclosure zone chimpanzees occupy may influence how shade is utilized, were included as random factors (random intercepts only) in the model.

For all generalized linear analyses, Wald χ^2 analysis of deviance type III testing was used to determine categorical predictor significance. For the GLMZ, the interaction effect of time*tertile was a significant predictor of sun and shade utilization (Wald $\chi^2_8 = 62.182$; $p < 0.001$) but, as β-estimate contrasts for the GLMZ (Appendix 3) did not distinguish between all within-group interactions, two separate GLZ analyses using the *glm* function of sun and shade selections were conducted to assess all within-group interaction contrasts. The first GLZ compared time of day differences within each tertile, using time of day as the categorical predictor while the second GLZ compared tertiles within time periods, using shade tertile as the categorical predictor. Both GLZ analyses used the counts of individuals in the sun and shade as a combined response variable.

Results

The results of the χ^2 test suggested that the chimpanzees were utilizing shade at significantly higher levels than expected by an equal sun: shade utilization pattern (χ^2_1 = 352.595; $p < 0.001$; Sun: 1262; Shade: 2398; expected equality: 1830).

Behaviour was a good predictor of the respective levels of sun and shade utilization (Wald χ^2_3 = 93.86; $p < 0.001$; β-estimates: Appendix 2). Of all the behaviours tested (Figure 3), the relative levels of sun: shade utilization were significantly greater for the active and inactive behaviour categories than social and other behaviours meaning that both the active and inactive categories were more sun- than shade-biased.

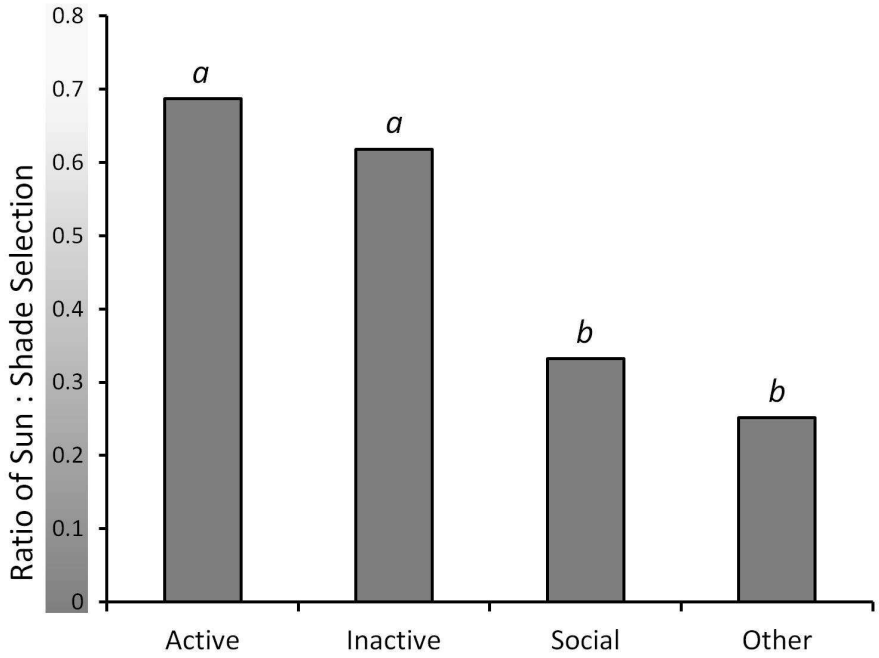

Figure 3. The ratio of sun: shade selection by a group of chimpanzees at the Johannesburg Zoo, South Africa, with regard to four behaviour categories. Darker y-axis shading (dark grey) reflects selection for shade utilization while lighter shading (light grey) reflects more sun utilization. Different lower case letters above bars denote statistically significant differences ($p < 0.05$).

The GLZ analysis of shade availability over the hours of the day indicated that time of day was a significant predictor of shade availability (Wald χ^2_4 = 14.302; p = 0.006; β-estimates: Appendix 3). The number of zones representing the high shade tertile was highest during the morning hours and late in the afternoon, with more low shade tertile zones occurring during midday. Inactivity was most sun-biased at 10h00, becoming increasingly shade biased around midday and then becoming sun-biased again around 14h00 (Figure 4). The GLMZ analysis revealed time of day (Wald χ^2_4 = 58.063; $p < 0.001$; β-estimates: Appendix 1) to be a good predictor of sun and shade utilization, regardless of the behaviour

performed (Figure 5). Chimpanzees spent more time in the sun than shade at the 10h00 sampling period, but more time in shade than sun between 11h00 and 14h00. Shade utilization was highest during the 12h00 hour.

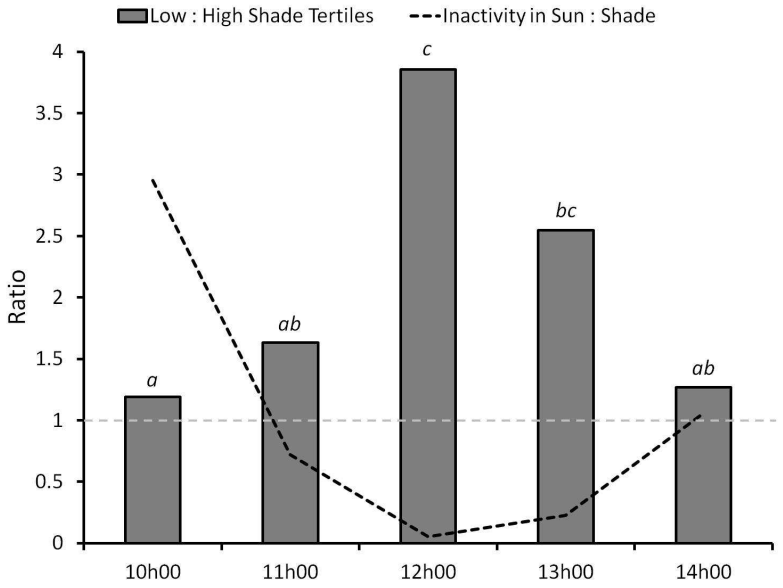

Figure 4. The ratios of low: high shade tertile zones throughout the chimpanzee enclosure at the Johannesburg Zoo, South Africa. The dashed black line is the ratio of sun: shade for inactivity scores exhibited by the chimpanzee group for the same period. The dashed light-grey line indicates an even availability of low and high shade tertile zones within the enclosure. Different lower case letters above the bars denote statistically significant differences ($p < 0.05$) for shade availability between time periods only.

Shade tertile alone (Wald $\chi^2_1 = 0.845$; $p = 0.358$) was not a good predictor of sun and shade utilization but the time*tertile interaction effect (Wald $\chi^2_4 = 34.701$; $p < 0.001$) was a significant predictor of sun and shade utilization (β-estimates: Appendices 4, 5 and 6). The differences between time periods for each tertile are shown in Figure 6 and Figure 7. Within the low shade tertile zones, shade-utilization was greatest during the 12h00 period and lowest around 10h00. In the high shade tertile zones, shade use was greatest at 13h00 but lowest at 12h00. For all times, the shade-utilization patterns in low and high tertiles were significantly different with significantly more shade utilization in high than low tertile zones in all time slots except 12h00, where shade utilization was significantly higher in low shade tertile zones. Minimum daily temperature was a predictor (Wald $\chi^2_1 = 63.987$; $p < 0.001$) but maximum daily temperature was not a predictor (Wald $\chi^2_1 = 0.026$; $p = 0.872$) of sun: shade utilization. However, the relationship between minimum daily temperature and sun: shade utilization was weak (Sun $R^2 = 0.0256$; Shade $R^2 = 0.0069$; Figure 8 and Figure 9), indicating that while statistically significant, the maximum and minimum temperatures were not good predictors of overall shade utilization patterns.

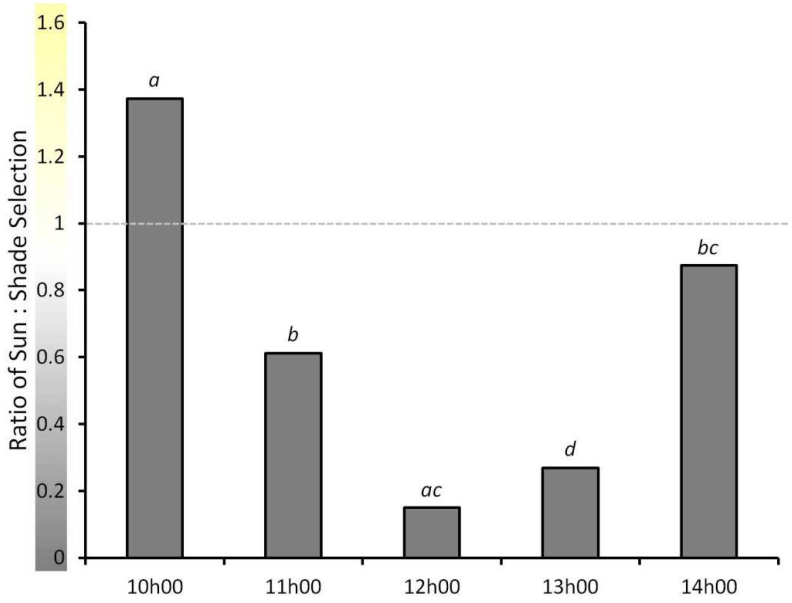

Figure 5. Ratio of sun: shade selection by a group of chimpanzees at the Johannesburg Zoo, South Africa. Darker y-axis shading (dark grey) reflects selection for shade and the lighter shading (yellow) reflects more sun utilization. Ratios of 1 suggest equal sun and shade selection, as represented by the dashed light-grey line. Alphabets above bars denote statistically significant differences ($p < 0.05$) between time periods.

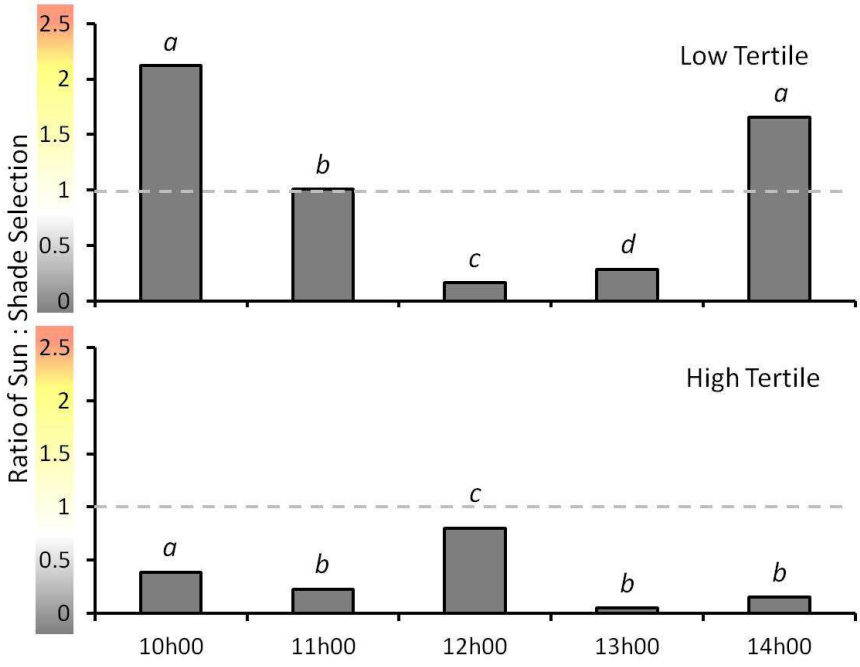

Figure 6. Ratio of sun: shade selection by a group of chimpanzees at the Johannesburg Zoo, South Africa, for two measures of shade availability, divided into low (top panel) and high (bottom panel) shade tertiles. Darker y-axis shading (dark grey) reflects selection for shade utilization while lighter shading (yellow to pink) reflects more sun utilization. Ratios of 1 suggest equal sun and shade selection, as represented by the dashed light-grey lines. Alphabets above bars denote statistically significant differences ($p < 0.05$) between times for each tertile.

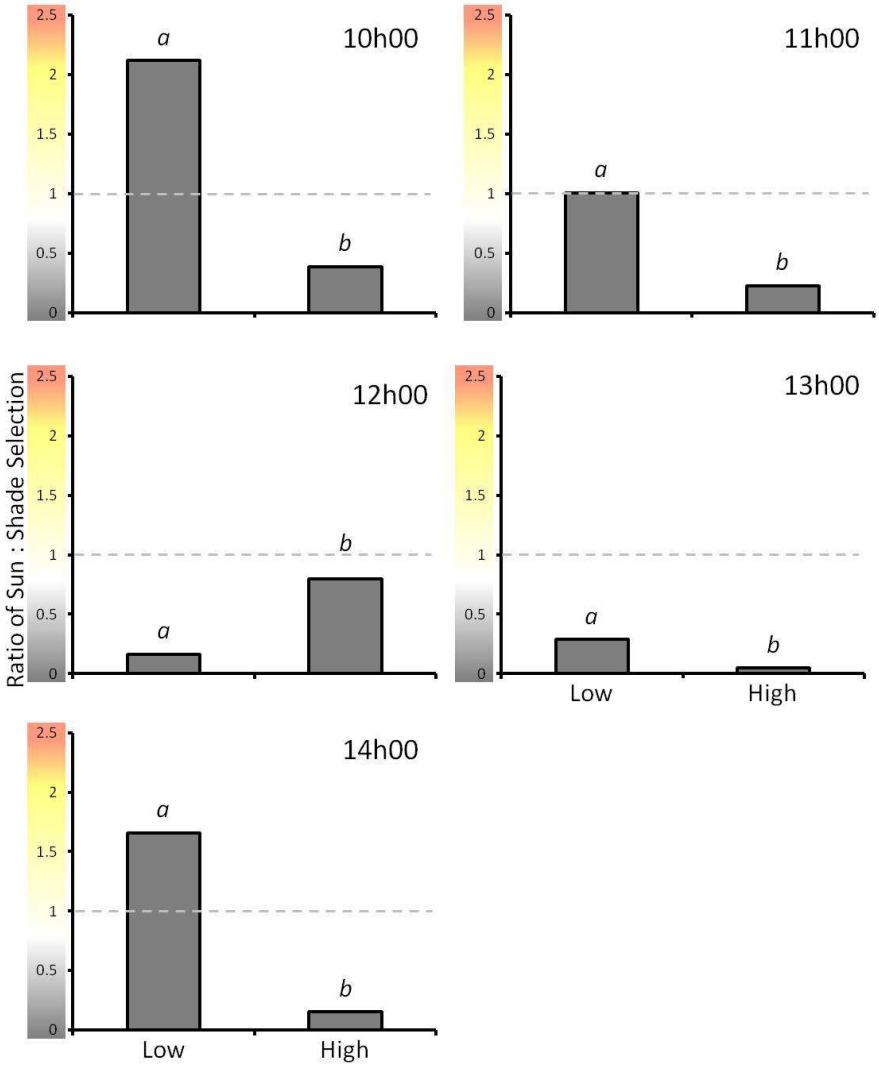

Figure 7. Ratio of sun: shade selection by a group of chimpanzees for different time periods at the Johannesburg Zoo, South Africa, for specific measures of shade availability, divided into low and high shade tertiles. Darker y-axis shading (dark grey) reflects selection for shade utilization while lighter shading (yellow to pink) reflects more sun utilization. Ratios of 1 suggest equal sun and shade selection, as represented by the dashed light-grey lines. Alphabets above bars denote statistically significant differences ($p < 0.05$) between tertiles for each time period

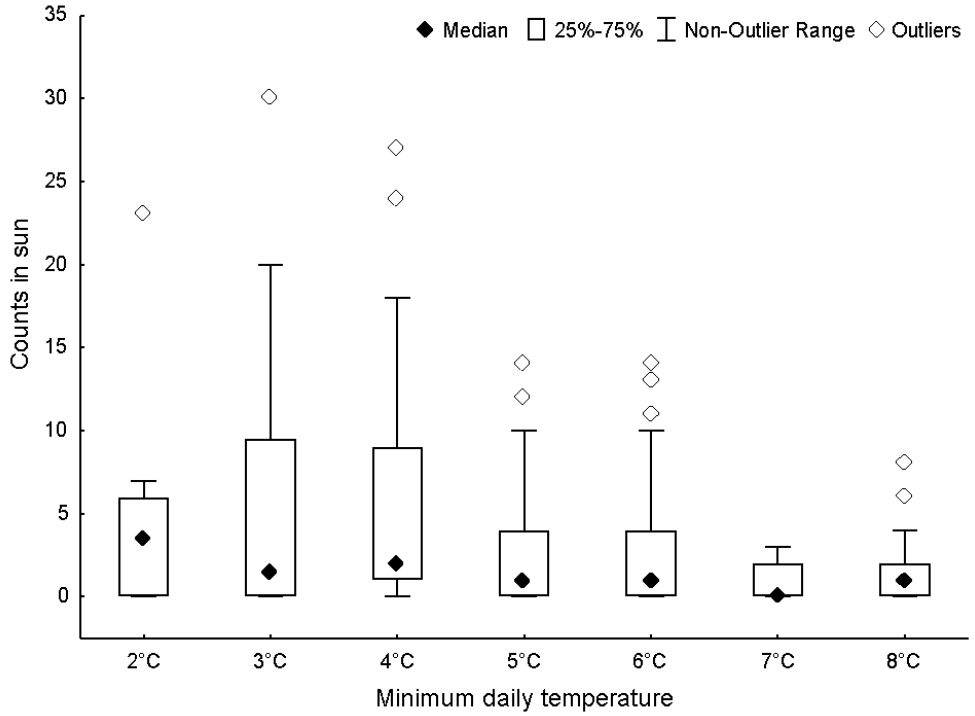

Figure 8. Spread of data for counts of observations of chimpanzees in the sun at the Johannesburg Zoo, South Africa, in relation to the full range of minimum daily temperatures (in degrees Celsius) recorded over the study period, following the identification of minimum daily temperature as a significant predictor of sun and shade utilization ($p < 0.05$)

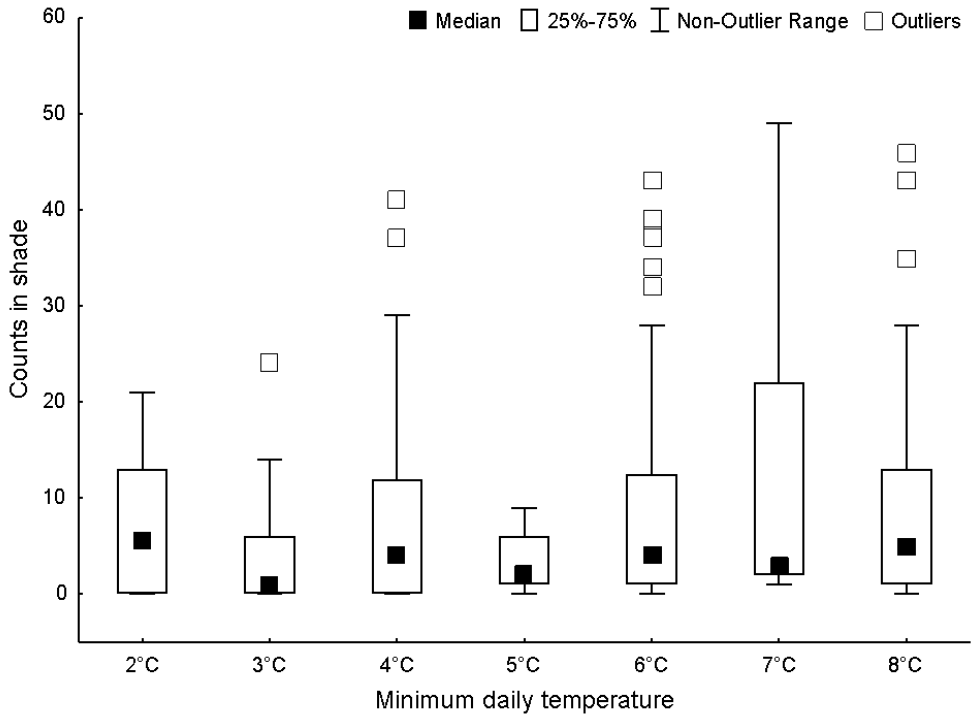

Figure 9. Spread of data for counts of observations of chimpanzees in the shade at the Johannesburg Zoo, South Africa, in relation to the full range of minimum daily temperatures (in degrees Celsius) recorded over the study period, following the identification of minimum daily temperature as a significant predictor of sun and shade utilization ($p < 0.05$)

Discussion

The aim of my study was to examine how chimpanzees utilize shade as a means of behavioural thermoregulation in a captive setting. I predicted that the chimpanzees at the Johannesburg Zoo would not utilize shade as often as direct sun, based on the differences between the winter/spring climates of the Johannesburg Zoo and the equatorial rainforest and grassland habitats of free-ranging chimpanzees and the limits of the chimpanzee thermal neutral zone. This prediction was not met as the chimpanzees appear to utilize shade at significantly higher levels than direct sunlight. In agreement with my findings, free-ranging chimpanzees spend relatively little time in direct sun (Kosheleff & Anderson, 2009) and captive gorillas *Gorilla gorilla gorilla* appear to preferentially spend more time in shade than direct sun (Stoinski *et al.*, 2001b). Surprisingly, given the differences between the climates at the Johannesburg Zoo and the equatorial rainforests, the same preference for shade over direct sun emerged. There are 2 possible explanations for this result.

1) On the one hand, the chimpanzees may have acclimatised to the climatic conditions at the Johannesburg Zoo, effectively tolerating lower ambient temperatures in Johannesburg than their free-ranging counterparts in equatorial regions. Primates should ideally be housed under climatic conditions similar to their natural environment (Coe, 1989), but for outdoor exhibits this is not feasible. Such housing under unnatural conditions could result in either pathology or a tolerance for the unnatural conditions. Lewis (1973) reported acclimatisation to captivity of 47216 individual Crab-eating macaques *Macaca fascicularis* and Rhesus macaques *Macaca mulatta* within 12 weeks, suggesting that primates do cope in new environments. However, this estimate is based on two measures of mortality and it is unclear whether there was a physiological response in the surviving individuals. How animals react to unnatural thermal conditions is uncertain (Lindburg, 1998) and further work is needed to examine whether or not captive primates acclimatise to environments outside their natural range.

2) Alternatively, it is possible that chimpanzees avoid direct sunlight regardless of ambient temperature. Solar radiation is likely to influence the behaviour of animals in open environments (Hill *et al.*, 2004) especially for animals with dark skin or hides (Young, 1982; Acharya *et al.*, 1995; Kosheleff & Anderson, 2009). Chimpanzee pelage offers limited insulation against solar radiation (Kosheleff & Anderson, 2009) but as the chimpanzee group at the Johannesburg Zoo frequently engage in hair plucking, a form of abnormal behaviour which exposes the dark skin (Walsh *et al.*, 1982), any exposure to direct sun, however brief,

is likely to result in rapid heat gain. Under such conditions, the chimpanzees are likely to avoid direct sunlight as the rapid heat gain may make the risk of overheating too great. Feedlot cattle in Arizona appear to adopt a similar strategy, resting in shade from as early as 07h00, approximately an hour after sunrise, and remaining in shade until approximately 17h00 (Ray & Roubicek, 1971). Given that ambient temperatures are unlikely to exceed the thermal neutral zone of cattle within an hour of sunrise, these results suggest that shade utilization in cattle may be a response to light intensity rather than ambient temperature (Finch, 1976). The chimpanzees seem to be adopting a similar strategy.

If the chimpanzees are indeed avoiding direct sunlight, temperature should not be a good predictor of sun and shade utilization because direct exposure to sunlight will result in heat gain irrespective of ambient thermal conditions. Only minimum daily temperature was a significant predictor of utilization patterns. However, Figure 8 and Figure 9 suggest that any relationship between minimum temperature and sun/shade utilization is weak at best. The pelage of chimpanzees does not appear to function in heat conservation (Benedict & Bruhn, 1936) and given the natural habitat of the species (Vigilant, 2004), it is not surprising that minimum temperature would influence behaviour. Minimum temperature also appears to influence behavioural thermoregulation of both free-ranging baboons (Barrett *et al.*, 2004) and Japanese macaques (Zhang *et al.*, 2007) as well as captive long-tailed macaques (Schino & Troisi, 1990) but why the relationship emerges as weak in this study is unclear. It is possible that the temperatures experienced at Johannesburg Zoo were not low enough to have a pronounced effect on the behaviour of the chimpanzees or alternatively the chimpanzees may have acclimated, but these ideas require further investigation.

While daily maximum temperature was not a good predictor of shade utilization, the patterns of inactivity over the day suggest that the chimpanzees are still sensitive to high temperatures. Inactivity occurred almost exclusively in the shade during the hottest hours of the day, while during 10h00 sampling period inactivity was more sun-biased. Free-ranging chimpanzees engage in more sedentary activities (Kosheleff & Anderson, 2009) and utilize caves (Pruetz, 2007) during midday and a number of baboon studies have highlighted that midday high temperatures are associated with reduced activity and increased shade seeking (Stelzner, 1988; Hill *et al.*, 2004; Hill, 2006a; Hill, 2006b).

While it seems logical to assume these patterns of inactivity and shade utilization are in response to changing temperatures, they should be interpreted cautiously as a number of other factors may also be at play. The chimpanzees were provided with food, scattered throughout the enclosure, at 10h00 to encourage them to leave the night rooms and thus may

have spent more time in the sun than during other time periods simply because of foraging. Alternatively, as the night rooms are not heated nor do they provide much sunlight, the chimpanzees may be inactive in the sun to warm up, much like morning sunbathing in other primate species (Young, 1982; Brockman *et al.*, 1987). It is also possible that non-thermoregulatory circadian effects may influence the patterns of shade utilization. Java monkeys appear to regulate autogrooming (Troisi & Schino, 1987) and chimpanzee (Kosheleff & Anderson, 2009) and human activity (Binkley, 1992) may vary according to non-thermal circadian patterns.

The chimpanzees also appeared to show a similar bias toward shaded zones over time for both low and high shade tertile zones. The 12h00 high tertile sun-use bias may be anomalous because of the small sample of high tertiles for that period consisted of only three observations, as most observations over that time period were excluded due to overcast conditions. If the 12h00 high tertile data point is excluded, the patterns are similar for both the High and Low tertiles, suggesting that the chimpanzees are preferentially utilizing shade throughout the sampling period regardless of how much shade is available. Furthermore, while shade was not absent around 12h00, the chimpanzees appear to still show a marked preference for shade even though little shade was available under trees during the midday period, with the sun directly overhead. Together, these results suggest that the chimpanzees are highly motivated to utilize shade during this period. Schütz *et al.* (2008) examined how motivated cattle, deprived of space to lie down, were to utilize shade by providing a choice between a high shade area and an area conducive to lying down and found that cattle opted to stand in the shade, rather than lie down, as ambient temperatures increased. Bohm Jr. *et al.* (2009) suggest that shade may be used as a tool to encourage captive primates to engage with particular elements of their enclosures, thereby suggesting that shade is an inherently valuable resource to captive primates.

The findings of Schütz *et al.* (2008) and suggestion of Bohm Jr. *et al.* (2009), together with the findings of my study, suggest that a lack of available shade may be cause for concern for animal welfare by placing animals at risk of physiological stress and overheating. While it is important that animals are presented with realistic thermal variation (Lindburg, 1998), my findings suggest that even naturalistic enclosures may not meet the biological needs of the animals (Fàbregas *et al.*, 2011), undermining their wellbeing (Maple & Finlay, 1989). Given that naturalistic enclosure designs are rapidly becoming the norm for captive environments (Maple & Finlay, 1989; Fàbregas *et al.*, 2011), and the expensive nature of their construction

and maintenance (Coe, 1989), it becomes increasingly important that enclosures are designed from a multifaceted functional as well as aesthetic standpoint (Little & Sommer, 2002).

In conclusion, this study examined the potential utilization of shade as a thermoregulatory strategy of captive chimpanzees. The chimpanzees appear to employ a sun-avoidance strategy for most of their time outdoors, despite experiencing relatively low environmental temperatures at the Johannesburg Zoo. Shade was actively utilized at higher levels than direct sun. While the level of available shade does not appear to influence shade utilization, the chimpanzees appear to selectively utilize shade more during the midday period than at other times, apparently in response to higher midday temperatures, but alternative explanations for this pattern must be explored in future. The results suggest that shade can constitute a valuable environmental resource for captive primates, promoting both physiological and behavioural welfare.

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Appendices: Tables of beta estimates calculated for generalized linear model analyses

Appendix 1. Beta estimates with standard errors and *p*-values generated through a Generalized linear mixed model (GLMZ) for contrasts between different time periods, coded by the approximate starting time for each hour (10h00-14h00), comparing sun and shade utilization of a group of captive chimpanzees at the Johannesburg Zoo, South Africa. Contrasts for which $p \leq 0.05$ appear in bold within grey cells

	10h00	11h00	12h00	13h00	14h00
10h00		**β = 1.54 ± 0.244; p < 0.005**	β = -0.02 ± 0.778; p = 0.983	**β = 4.27 ± 0.782; p < 0.005**	**β = 1.35 ± 0.438; p < 0.005**
11h00	**β = -1.54 ± 0.244; p < 0.005**		**β = -1.56 ± 0.773; p = 0.044**	**β = 2.73 ± 0.766; p < 0.005**	β = -0.2 ± 0.443; p = 0.655
12h00	β = 0.02 ± 0.778; p = 0.983	**β = 1.56 ± 0.773; p = 0.044**		**β = 4.29 ± 1.065; p < 0.005**	β = 1.36 ± 0.861; p = 0.114
13h00	**β = -4.27 ± 0.782; p < 0.005**	**β = -2.73 ± 0.766; p < 0.005**	**β = -4.29 ± 1.065; p < 0.005**		**β = -2.92 ± 0.856; p < 0.005**
14h00	**β = -1.35 ± 0.438; p < 0.005**	β = 0.2 ± 0.443; p = 0.655	β = -1.36 ± 0.861; p = 0.114	**β = 2.92 ± 0.856; p < 0.005**	

Appendix 1. Beta estimates with standard errors and *p*-values generated in a generalized linear model (GLZ) for pairwise contrasts between different behaviour categories, comparing sun and shade utilization of a group of captive chimpanzees at the Johannesburg Zoo, South Africa. Contrasts for which $p \leq 0.05$ appear in bold within grey cells

	Active	Inactive	Social	Other
Active		*β* = -0.38 ± 0.067; *p* = 0.198	**β = -1.00 ± 0.121; p < 0.005**	**β = -0.73 ± 0.138; p < 0.005**
Inactive	*β* = 0.38 ± 0.067; *p* = 0.198		**β = -0.9 ± 0.112; p < 0.005**	**β = -0.62 ± 0.130; p < 0.005**
Social	**β = 1.00 ± 0.121; p < 0.005**	**β = 0.9 ± 0.112; p < 0.005**		*β* = -0.28 ± 0.157; *p* = 0.079
Other	**β = 0.73 ± 0.138; p < 0.005**	**β = 0.62 ± 0.130; p < 0.005**	*β* = 0.28 ± 0.157; *p* = 0.079	

Appendix 2. Beta estimates with standard errors and *p*-values generated in a generalized linear model (GLZ) for pairwise contrasts between different hour-long time periods, comparing shade availability, coded as the number of low tertile zones (zones identified as < 30% shaded) and high tertile zones (zones identified as > 70% shaded) in a chimpanzee enclosure at the Johannesburg Zoo, South Africa. Contrasts for which $p \leq 0.05$ appear in bold within grey cells

	10h00	11h00	12h00	13h00	14h00
10h00		*β* = 0.32 ± 0.288; *p* = 0.272	***β* = 1.18 ± 0.366; *p* < 0.005**	***β* = 0.76 ± 0.298; *p* = 0.011**	*β* = 0.06 ± 0.404; *p* = 0.878
11h00	*β* = -0.32 ± 0.288; *p* = 0.272		*β* = 0.86 ± 0.36; *p* = 0.272	***β* = 0.44 ± 0.290; *p* = 0.017**	*β* = -0.25 ± 0.4; *p* = 0.522
12h00	***β* = -1.18 ± 0.366; *p* < 0.005**	*β* = -0.86 ± 0.36; *p* = 0.272		*β* = -0.41 ± 0.368; *p* = 0.259	***β* = -1.11 ± 0.457; *p* = 0.015**
13h00	***β* = -0.76 ± 0.298; *p* = 0.011**	***β* = -0.44 ± 0.290; *p* = 0.017**	*β* = 0.41 ± 0.368; *p* = 0.259		*β* = -0.7 ± 0.405; *p* = 0.085
14h00	*β* = -0.06 ± 0.404; *p* = 0.878	*β* = 0.25 ± 0.4; *p* = 0.522	***β* = 1.11 ± 0.457; *p* = 0.015**	*β* = 0.73 ± 0.138; *p* < 0.006	

Appendix 4. Beta estimates with standard errors and *p*-values generated in a generalized linear mixed model (GLMZ) for pairwise contrasts within a time*tertile interaction effect, specifically comparing sun and shade utilization of a group of captive chimpanzees at the Johannesburg Zoo, South Africa, for all time periods within the low tertile zones (zones identified as < 30% shaded) to all times within the high tertile zones (zones identified as > 70% shaded). Time of day comprised five hour-long periods, coded by the approximate starting time for each hour (10h00-14h00) and available amount of shade was coded as two levels of a tertile shade estimation (low, high). Contrasts for which $p \leq 0.05$ appear in bold within grey cells

		High				
		10h00	11h00	12h00	13h00	14h00
Low	10h00		**β = 1.03 ± 0.286; p < 0.005**	**β = -2.26 ± 0.799; p < 0.005**	**β = 2.38 ± 0.792; p < 0.005**	**β = 1.72 ± 0.494; p < 0.005**
	11h00	**β = -1.03 ± 0.286; p < 0.005**		**β = -3.29 ± 0.796; p < 0.005**	β = 1.35 ± 0.778; p = 0.083	β = 0.69 ± 0.504; p = 0.17
	12h00	**β = 2.26 ± 0.799; p < 0.005**	**β = 3.29 ± 0.796; p < 0.005**		**β = 4.64 ± 1.079; p < 0.005**	**β = 3.99 ± 0.898; p < 0.005**
	13h00	**β = -2.38 ± 0.792; p < 0.005**	β = -1.35 ± 0.778; p = 0.083	**β = -4.64 ± 1.079; p < 0.005**		β = -0.66 ± 0.884; p = 0.456
	14h00	**β = -1.72 ± 0.494; p < 0.005**	β = -0.69 ± 0.504; p = 0.17	**β = -3.99 ± 0.898; p < 0.005**	β = 0.66 ± 0.884; p = 0.456	

Appendix 5. Beta estimates with standard errors and *p*-values generated in a generalized linear mixed model (GLMZ) for pairwise contrasts within a time*tertile interaction effect, specifically comparing sun and shade utilization of a group of captive chimpanzees at the Johannesburg Zoo, South Africa, for all time periods within the high tertile zones (zones identified as > 70% shaded) to all times within the low tertile zones (zones identified as < 30% shaded). Time of day comprised five hour-long periods, coded by the approximate starting time for each hour (10h00-14h00) and available amount of shade was coded as two levels of a tertile shade estimation (low, high). Contrasts for which $p \leq 0.05$ appear in bold within grey cells

		Low				
		10h00	11h00	12h00	13h00	14h00
High	10h00		**β = -1.03 ± 0.286; p < 0.005**	**β = 2.26 ± 0.799; p < 0.005**	**β = -2.38 ± 0.792; p < 0.005**	**β = -1.72 ± 0.494; p < 0.005**
	11h00	**β = 1.03 ± 0.286; p < 0.005**		**β = 3.29 ± 0.796; p < 0.005**	β = -1.35 ± 0.778; p = 0.083	β = -0.69 ± 0.504; p = 0.17
	12h00	**β = -2.26 ± 0.799; p < 0.005**	**β = -3.29 ± 0.796; p < 0.005**		**β = -4.64 ± 1.079; p < 0.005**	**β = -3.99 ± 0.898; p < 0.005**
	13h00	**β = 2.38 ± 0.792; p < 0.005**	β = 1.35 ± 0.778; p = 0.083	**β = 4.64 ± 1.079; p < 0.005**		β = 0.66 ± 0.884; p = 0.456
	14h00	**β = 1.72 ± 0.494; p < 0.005**	β = 0.69 ± 0.504; p = 0.17	**β = 3.99 ± 0.898; p < 0.005**	β = -0.66 ± 0.884; p = 0.456	

Appendix 6. Beta estimates with standard errors and *p*-values generated in a generalized linear model (GLZ) used to identify specific pairwise contrasts for a generalized linear mixed model (GLMZ) time*tertile interaction effect, specifically comparing sun and shade utilization of a group of captive chimpanzees at the Johannesburg Zoo, South Africa, for all time periods within the low tertile zones (zones identified as < 30% shaded). Time of day comprised five hour-long periods, coded by the approximate starting time for each hour (10h00-14h00). Contrasts for which $p \leq 0.05$ appear in bold within grey cells

		Low				
		10h00	11h00	12h00	13h00	14h00
Low	10h00		**β = -0.74 ± 0.127; p < 0.005**	**β = -2.55 ± 0.153; p < 0.005**	**β = -2 ± 0.127; p < 0.005**	β = -0.25 ± 0.206; p = 0.235
	11h00	**β = 0.74 ± 0.127; p < 0.005**		**β = -1.81 ± 0.152; p < 0.005**	**β = -1.25 ± 0.125; p < 0.005**	**β = 0.5 ± 0.205; p = 0.015**
	12h00	**β = 2.55 ± 0.153; p < 0.005**	**β = 1.81 ± 0.152; p < 0.005**		**β = 0.56 ± 0.151; p < 0.005**	**β = 2.31 ± 0.222; p < 0.005**
	13h00	**β = 2 ± 0.127; p < 0.005**	**β = 1.25 ± 0.125; p < 0.005**	**β = -0.56 ± 0.151; p < 0.005**		**β = 1.75 ± 0.205; p < 0.005**
	14h00	β = 0.25 ± 0.206; p = 0.235	**β = -0.5 ± 0.205; p = 0.015**	**β = -2.31 ± 0.222; p < 0.005**	**β = -1.75 ± 0.205; p < 0.005**	

Appendix 7. Beta estimates with standard errors and *p*-values generated in a generalized linear model (GLZ) used to identify specific pairwise contrasts for a generalized linear mixed model (GLMZ) time*tertile interaction effect, specifically comparing sun and shade utilization of a group of captive chimpanzees at the Johannesburg Zoo, South Africa, for all time periods within the high tertile zones (zones identified as > 70% shaded). Time of day comprised five hour-long periods, coded by the approximate starting time for each hour (10h00-14h00). Contrasts for which $p \leq 0.05$ appear in bold within grey cells

		High				
		10h00	11h00	12h00	13h00	14h00
High	10h00		**β = -0.55 ± 0.205; p = 0.007**	**β = 0.73 ± 0.686; p = 0.290**	**β = -2.12 ± 0.738; p < 0.005**	**β = -0.92 ± 0.369; p = 0.012**
	11h00	**β = 0.55 ± 0.205; p = 0.007**		**β = 1.27 ± 0.687; p = 0.064**	β = -1.57 ± 0.738; p = 0.032	β = -0.38 ± 0.370; p = 0.308
	12h00	**β = -0.73 ± 0.686; p = 0.290**	**β = -1.27 ± 0.687; p = 0.064**		**β = -2.85 ± 0.987; p < 0.005**	**β = -1.65 ± 0.752; p = 0.028**
	13h00	**β = 2.1 ± 0.738; p < 0.005**	β = 1.57 ± 0.738; p = 0.032	**β = 2.85 ± 0.987; p < 0.005**		β = 1.2 ± 0.799; p = 0.134
	14h00	**β = 0.92 ± 0.369; p = 0.012**	β = 0.38 ± 0.370; p = 0.308	**β = 1.65 ± 0.752; p = 0.028**	β = -1.2 ± 0.799; p = 0.134	

Appendix 8. Beta estimates with standard errors and *p*-values generated through a generalized linear model (GLZ) used to identify specific pairwise contrasts for a generalized linear mixed model (GLMZ) time*tertile interaction effect, specifically comparing sun and shade utilization in Low (zones identified as < 30% shaded) and High tertile zones (zones identified as > 70% shaded) at each time period by a group of captive chimpanzees at the Johannesburg Zoo, South Africa. Time of day comprised five hour-long periods, coded by the approximate starting time for each hour (10h00-14h00). Contrasts for which $p \leq 0.05$ appear in bold within grey cells

		Low
10h00	High	**β = -0.59 ± 0.202; p < 0.005**
11h00		**β = 1.50 ± 0.171; p < 0.005**
12h00		**β = 0.19 ± 0.561; p = 0.731**
13h00		**β = 1.82 ± 0.729; p = 0.012**
14h00		**β = 2.38 ± 0.387; p < 0.005**

	High
Low	**β = 0.59 ± 0.202; p < 0.005**
	β = -1.50 ± 0.171; p < 0.005
	β = -0.19 ± 0.561; p = 0.731
	β = -1.82 ± 0.729; p = 0.012
	β = -2.38 ± 0.387; p < 0.005

Chapter 6. General discussion

Overview

Animals in captive environments experience conditions which are beyond their control. These imposed conditions, directly or indirectly, lead to stress in captive animals. The aim of my study was to investigate how chimpanzees, a species that exhibits extensive behavioural flexibility, high intelligence and complex sociality, respond to changes imposed within a zoo environment. The experiments described in my study exploited the opportunistic changes in husbandry and management protocols imposed by the Johannesburg Zoo. My research focused on four aspects of chimpanzee captive maintenance: responses to long-term spatial restriction, the long-term effects of spatial change on space use and group spacing, the effects of social change and the role of shade as a thermoregulatory resource for captive chimpanzees. Each of these investigations is novel in its own right, and revealed many complex and subtle ways in which changes in captivity influence chimpanzees and how chimpanzees respond to these conditions.

Overall, in my studies, the chimpanzees responded to spatial change through flexibility, employing different behavioural strategies to respond to the social stress of long-term spatial restriction. My findings supported the coping model (de Waal, 1989) and suggested that abnormal behaviour may function as an outlet for stress during long-term spatial restriction. Five years after the enclosure change, the chimpanzees displayed a consistent pattern of limited space use and tight group spacing, contingent on previous housing dimensions which was not adequately explained by climatic, temporal, behavioural, social, visitor or environmental feature effects in the current environment. I suggested that a likely explanation appears to be a form of spatial learned helplessness, resulting from the spatial restriction of the previous housing condition. The chimpanzees displayed variable qualitative and quantitative behavioural and social shifts in response to species-typical social manipulations at the zoo. However, the removal of an adult female appeared to have been less disruptive than the merging of two existing social groups, as indicated by less stress-related behaviour in the former manipulation. Finally, within the new enclosure, shade appeared to function as a valuable thermal resource for the chimpanzees. Despite my study taking place during the austral winter, the chimpanzees selectively spent time in shade, avoiding direct sunlight.

In the sections that follow, I describe the current understanding of the stress response in captivity and propose a more comprehensive model for examining the responses of chimpanzees to the imposed stressors of the captive environment. I discuss my findings in relation to my proposed model as well as the existing literature, highlighting inconsistencies and potential gaps in the literature. Finally, I identify areas for future research and suggest directions for further study.

The stress response in the captive environment

Various aspects of the physical environment in captivity may be stressful for animals (Morgan & Tromborg, 2007). The current view of the stress response of animals in captivity (e.g. Tennessen, 1989) suggests that the behavioural response to stressors of animals is determined by the current environment and the nature of the stressor. Unnatural conditions (Morgan & Tromborg, 2007) and a lack of control in the captive environment cause animals to be stressed and animals then respond by either utilizing their inherent flexibility to restore allostasis or, failing which, exhibit pathology (Clark *et al.*, 1997).

This understanding of the stress response is by no means incorrect, but fails to take into account the various factors which contribute to the behavioural motivation driving the responses to stress. The behavioural motivation of an individual. Motivation, the summation and interactions of internal and external stimuli that lead to the expression of behaviour (Barnard, 1995), is driven by both the immediate internal and external stimuli as well as individual variation and past experience (Jensen & Toates, 1993) but the description of stress response above assumes that animals are merely responding to the immediate stressor and current environmental conditions. I suggest, based on the findings of my studies, that a far more comprehensive approach to the stress response of captive animals is needed in order to better understand how captive environments influence the behaviour, and ultimately well-being, of animals.

Direct environmental influences on motivation

The captive environment influences the motivational state of an individual through two main avenues. Firstly, the environment either directly or indirectly generates the stressors that an individual faces (Morgan & Tromborg, 2007; encircled letter A, Figure 1). In addition, the captive environment limits the behavioural opportunities available to individuals (Altman, 1999) by limiting the degree of choice and control afforded to individuals (B,

Figure 1). The degree to which individuals can control their environment influences various proximate factors related to motivation. While the motivation of an animal cannot be measured *per se*, behavioural expression, in relation to the various factors discussed hereafter, assumes the underlying motivational state.

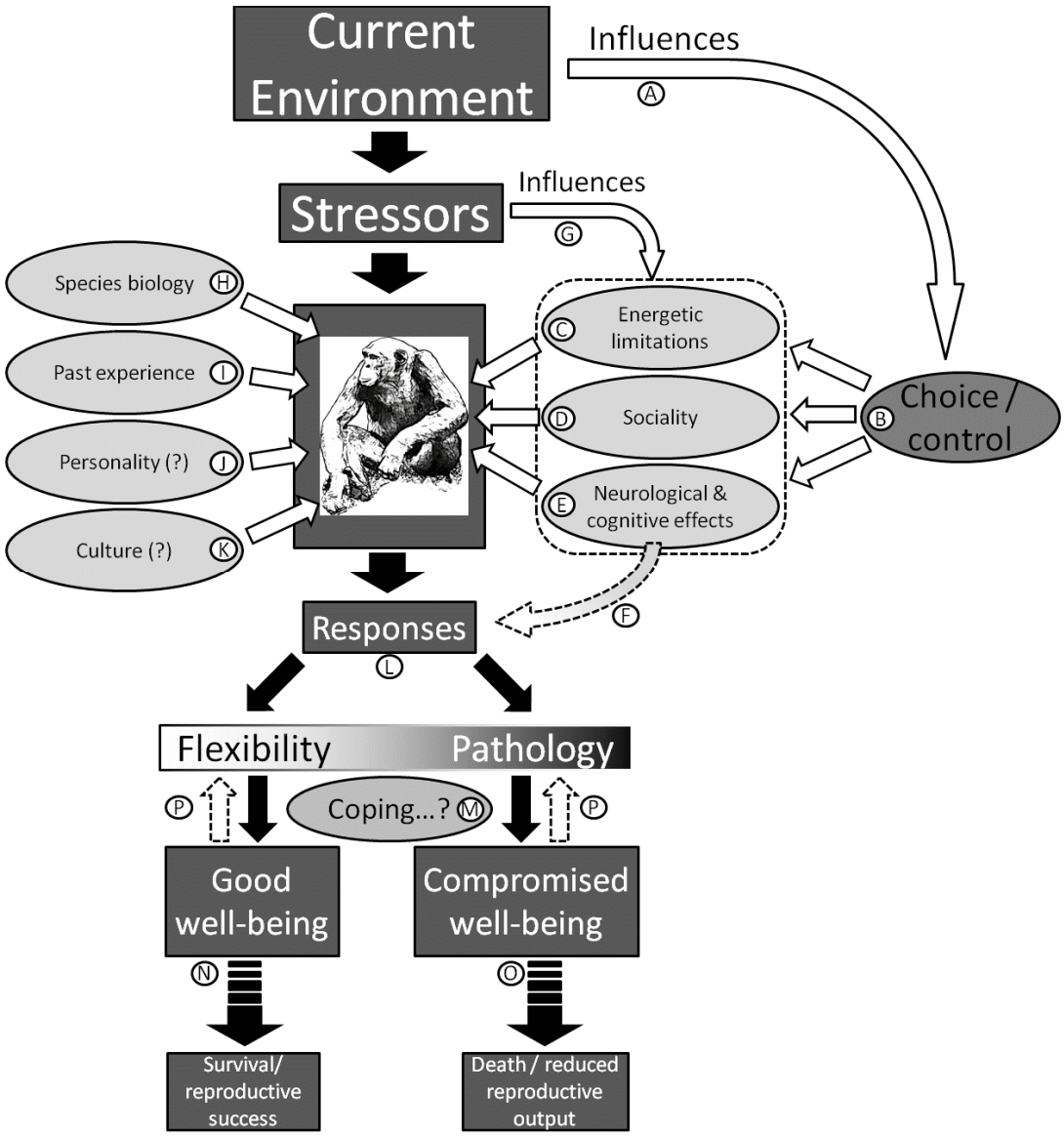

Figure 1. The influence of various factors on the behavioural motivation and expression of captive chimpanzees in response to environmentally-induced stress. The traditional view of the stress response (black arrows, blocks) suggests that the captive environment imposes stressors on chimpanzees, which respond through flexible behaviour resulting in restoration of allostasis and ultimately survival and reproductive success. If chimpanzees fail to respond flexibly, pathology may develop which compromises welfare leading to effects such as premature death or reduced reproductive output. However, various other aspects of the captive environment (white arrows, ovals) may contribute to the response to stressors. Other factors, such as the biology of the species, past experiences, personality and individual-specific effects and cultural transmission may further influence the stress responses. These proximate factors may act independently of or supersede more immediate causal influences, such as existing environmental conditions, in determining stress response in chimpanzees. Encircled letters are reference points to discussion in the text

Energetic constraints

Energetic constraints (C, Figure 1) function as internal stimuli which contribute to motivation based on energy intake through the food provided (Klingerman *et al.*, 2011) and energetic expenditure through metabolism (Schneider, 2004) and the energetic costs of performing behaviour (Young, 2003). In Chapter 5 of my study, the frequent shade utilization highlighted one of the subtle ways that a captive environment can limit or alter energetic constraints. The patterns of shade utilization suggest that the chimpanzees were motivated to utilize shade and the structure of the enclosure provided a choice for chimpanzees between rapid heat gain in the sun or a cooler microclimate in the shade. Given that behavioural thermoregulation is less energetically costly than physiological thermoregulation (Barton *et al.*, 1992), the choice between sun and shade allowed the pre-existing motivation for shade utilization to be expressed as shade-seeking behaviour.

Constraints of sociality

The limitations of social rules and hierarchy (Chapais & Larose, 1988) and the availability of social partners influence the sociality of captive animals (D, Figure 1). The presence of social partners influences which social partners individuals choose to interact with and what associated behaviour is expressed. For example, the presence of social partners is known to reduce the experience of stress in animals, a process termed social buffering (Hennessy *et al.*, 2009). In Chapter 4, the separation of the chimpanzees into single-sex groups clearly limited the social partners available to individuals and, following merging, social interactions between individuals underwent both qualitative and quantitative changes. However, an absence of individuals may also remove socially imposed limitations on behaviour. For example, the separation into two single-sex groups in my study may have facilitated the expression of aggression in the female group because the males may have mediated intra-group aggression, as occurs in free-ranging populations; male chimpanzees may intervene in female-female conflict (termed 'control-role' behaviour: Anderson *et al.*, 1977; Kahlenberg *et al.*, 2008).

The role of cognition

The environment influences brain and cognitive development (Gardner *et al.*, 1975; Turner & Lewis, 2003; Turner *et al.*, 2003) and as such, neurological and cognitive effects (E, Figure 1) are also likely to influence the behavioural motivations of individuals by

influencing the degree to which chimpanzees can respond flexibly. While not explicitly tested in my study, chimpanzees display advanced social cognition (Call, 2001; Tomasello *et al.*, 2003; Hare *et al.*, 2006) and the responses of the chimpanzees to spatial restriction in Chapter 2 suggest that social cognition can be utilized by chimpanzees as a tool to manage group aggression. Many studies have examined the role of chimpanzee cognition in tool manufacture and use with regard to enrichment design in particular (e.g. Celli *et al.*, 2003), but social cognition has received comparatively little attention outside the laboratory setting. How chimpanzee social cognition influences behavioural expression in nature is only beginning to be understood (Crockford *et al.*, 2012) and given that it is far easier to study captive animals than free-ranging populations (Rowell, 1967), it is peculiar that few studies of captive chimpanzee welfare and husbandry have considered the influence of social cognition on the responses to stressors.

Cognition may also play a larger role in chimpanzee behaviour than other species due to their high intelligence (see Chapter 1). Unlike other animal species, I believe that chimpanzees may utilize cognition as a 'motivational filter' (F, Figure 1) whereby cognitive processes may supersede the influence of other factors which contribute to motivation. For example, chimpanzees participating in a cumulative reward task display self-restraint, redirecting behaviour and attention away from the accumulating rewards in order to cope with impulsivity, thereby increasing their gained rewards (Evans & Beran, 2007). However, little research has examined the degree to which cognition can influence behavioural motivation and expression.

The type, and intensity of the stressor may have a direct influence on the degree to which energetic limitations, sociality and neuro-cognitive effects influence the stress response (G, Figure 1). For example, chimpanzees appear to better cope with changes to the social environment than changes to the physical environment (Reimers *et al.*, 2007). Thus, while the degree of choice and controllability influences behavioural responses to stress, these responses may also be influenced by the nature of the stressor the animal experiences.

Innate influences on motivation

The examples discussed thus far illustrate how current or proximate factors can influence behavioural responses to stressors. However, a variety of more subtle factors may influence the stress response in captivity. Various outcomes of my study suggest that these factors, which are typically independent of the current environment and are not mediated by the degree of choice and control, may be as, if not more, important than the proximate

elements already mentioned in driving motivation and behavioural expression in response to stress in captivity. I discuss these factors next.

Species biology

Many behavioural phenotypes may be directly under genetic control. For example, stereotypical behaviours in African striped mice *Rhabdomys pumilio* is genetically transmitted from mothers to offspring, which is uncoupled from the housing conditions of the animal (Schwaibold & Pillay, 2001; Jones *et al.*, 2008). In Chapter 5, the chimpanzees avoided direct sun, probably as a result of rapid heat gain due to their dark pelage (Kosheleff & Anderson, 2009). Thus, the chimpanzees were forced to display a particular pattern of behaviour due to physiological constraints imposed by the anatomy of the species. These examples illustrate how species biology may limit or constrain behaviour.

The biology of an animal also dictates the ability of individuals to respond to stimuli in a flexible way. Species biology has been considered as very important when designing environmental enrichment (Clubb & Mason, 2007) but how species biology may dictate flexibility in response to stress has not received much attention. Chimpanzees display extensive behavioural flexibility (Wallace, 1979) and flexible behavioural responses of individuals are important for restoring allostasis following exposure to a stressor (Clark *et al.*, 1997). The chimpanzees in my study displayed two flexible responses to stress. Selective social interactions between individuals were displayed in response to the social disruptions of group merging and the removal of an individual from the chimpanzee group (Chapter 4). Under spatial crowding, the chimpanzees displayed both tension-reduction and conflict-avoidance responses to the increased social tension associated with spatial crowding (Chapter 2). In both cases, the chimpanzees did not display one tactic in response to stress, but appear to have strategically employed multiple tactics depending on the context of the stressor they experienced. Other studies have also found that chimpanzees use behavioural flexibility in response to spatial crowding. Under differing conditions, a group of chimpanzees may exhibit tension-reduction responses (Nieuwenhuijsen & de Waal, 1982), conflict-avoidance responses (Aureli & de Waal, 1997) or both tension-reduction and conflict-avoidance responses (Videan & Fritz, 2007).

Many studies have overlooked the influence of species-typical effects on behavioural responses (H, Figure 1). This is particularly evident in the literature with regard to

environmental enrichment, where protocols are often applied from one species to another, without considering the relevance of the enrichment for the animals (e.g. Wells *et al.*, 2007).

Effects of past experience and learning

Past experience has been identified as a causal factor in determining the behaviour of chimpanzees (Nash *et al.*, 1999; Reimers *et al.*, 2007) and other primates (Mallapur & Choudhury, 2003). While it seems intuitive that past experience will have a direct influence on behaviour, few studies of captive animals have considered this effect. This may be because quantifying past experiences is very difficult in most cases. For example, the orphan chimpanzees in my study (Chapter 2) were of unknown origin or history as they were rescued by or donated to the Jane Goodall Institute South Africa. However, my study (Chapter 3) provides an example of a quantifiable past experience (the old housing condition) generating lasting, clearly evident effects on the spatial behaviour of the chimpanzees, which appear to meet the criteria for learned helplessness (Martin Seligman, Pers. Comm.).

The ontogeny and mechanisms behind the influence of past experiences, such as early handling or maternal separation, on stress response behaviour have been well studied in a variety of species, ranging from rodents to livestock (Anisman *et al.*, 1998; Braastad, 1998) but the mechanisms behind the emergence of learned helplessness (LH) effects are still unclear. The uncontrollability of the initial stimulus, which is important in the onset of LH (Seligman *et al.*, 1968), appears to alter activity of the hypothalamic-pituitary-adrenal (HPA) axis (Haracz *et al.*, 1988), and circulating monoamines in the prefrontal cortex and hippocampus have also been implicated in the LH effect (Sagen *et al.*, 1990; Petty *et al.*, 1994a; Petty *et al.*, 1994b; Eisenstein & Carlson, 1997). The HPA axis is typically associated with stress (Grissom & Bhatnagar, 2009; Sarabdjitsingh *et al.*, 2012) and therefore it is possible that the chimpanzees displayed spatial LH behaviour following the stress of spatial restriction.

From early on, LH was known to result in impaired learning, labeled as cognitive deficits (Maier & Seligman, 1976; Maier, 1980). LH mice exhibit lower levels of brain derived neurotrophic factor (BDNF) and cAMP-response element binding protein (CREB) gene expression in the hippocampus than control individuals (Song *et al.*, 2006). There is strong evidence that BDNF (Mu *et al.*, 1999; Kesslak *et al.*, 2003; Parnpiansil *et al.*, 2003; Nakajo *et al.*, 2008) and CREB (Goldbart *et al.*, 2003; Alvarez-Jaimes *et al.*, 2005; Wang *et al.*, 2008) gene expression improves spatial learning and memory in rodents. Thus,

individuals displaying LH are likely to exhibit impaired spatial learning as well. Woodlice *Porcellio scaber* and African striped mice exhibit limited movement patterns following housing in small environments (D'Egidio, 2012) and environmental novelty appears to be closely associated with LH behaviour (Padilla *et al.*, 2010); these examples suggest a further link between LH behaviour and the spatial domain. Thus, it is feasible that a complex interplay of environmental novelty, the stress and associated HPA activation of a change of enclosure and impaired spatial learning resulting from the previous housing condition generated, what I termed, the spatio-cognitive deficit (SCD) effects described for the chimpanzees in my study.

The spatial LH behaviour described for the chimpanzees in my study appeared to affect the space use and spacing of all individuals within the group. However, it was unclear whether all individuals within the group exhibited SCD or whether it manifested as a group-based phenomenon. That no social pairs were identified as good predictors of spacing, suggests that perhaps the effect was experienced by all individuals equally, but the possibility that the chimpanzees may have learned the behaviour from one another remains unexplored. It would be of interest to investigate whether the youngest member of the group, Charles, who never experienced the old enclosures, displays a similar pattern of limited space use as an adult. If so, this might suggest some form of cultural transmission (see *Cultural transmission effects* below) within the group, but if not, would suggest that LH is a plausible explanation for the observed space use and group spacing.

The results of my study also indicate that past experience is not only important, but may override current environmental conditions in determining behavioural motivation to use space. Suggestions that the behaviour exhibited may reflect behavioural or psychological scars (Swaisgood & Shepherdson, 2005) have been underplayed in the literature, but my study provides further evidence that these factors may have a fundamental role in the stress responses of captive animals (I, Figure 1).

Personality and individual-specific effects

While not explicitly tested by the experiments in my study, personality and individual-based effects, such as individual past experience and coping styles, are likely to influence the behavioural motivation of animals in response to stress. Animals exhibit substantial individual variation in response to stress (Honess & Marin, 2006; Avitsur *et al.*, 2007) and past experience and personality of individuals appear to influence the type of

pathology expressed when allostasis is compromised in chimpanzees (Walsh *et al.*, 1982). Coping styles, a term occasionally used synonymously with personality, specifically refer to patterns of individual variation exhibited in response to stress (Koolhaas *et al.*, 1999). The patterns of social interaction following merging and the individual removal in Chapter 5 of my study, suggested that the interactions of individuals are governed by individual choice, but may be mediated by the constraints of group social functioning. These patterns alone suggest that individual variation with regard to behavioural stress responses is important (J, Figure 1).

Cultural transmission effects

There are two avenues through which cultural transmission of behaviour (K, Figure 1) may affect the motivation and behaviour of chimpanzees in response to stress. Firstly, chimpanzees are the only animals for which teaching in captivity has potentially been demonstrated (Caro & Hauser, 1992) and apes are capable of complex learning and imitation (Bjorklund & Bering, 2003). Thus, there is the possibility that the behaviour of captive chimpanzees may be limited by the effects of learning responses from others. Individual chimpanzees may exhibit abnormal behaviour in captivity which has been learned from other chimpanzees (Hook *et al.*, 2002) and thus an abnormal behavioural response does not necessarily constitute a stress-related motivational outcome. Secondly, free-ranging chimpanzee populations display distinct cultural behavioural differences in nature (Boesch & Tomasello, 1998). These cultural differences are identified through population-specific idiosyncratic behavioural patterns (Vigilant, 2004) which typically serve a variety of functions. It is therefore feasible that captive chimpanzee groups may display patterns of behaviour entirely unrelated to the stressors to which they are exposed, in much the same way that learned behaviour may be decoupled from the stress response. However, testing for cultural influences on the stress responses of chimpanzees may be very difficult, given the complex interplay of other factors which drive the behavioural motivation of captive chimpanzees.

Behavioural responses to stress

The various factors which have been discussed thus far result in a behavioural response (L, Figure 1). When animals modify their behaviour flexibly in response to stress, the restoration of allostasis is considered as coping (Clark *et al.*, 1997). However, there are

various definitions of coping (Wechsler, 1995) and hereafter, I refer to coping as any behavioural response which minimizes the effects of a stimulus on individual well-being (Schouten & Wiepkema, 1991), as individual well-being influences individual fitness and reproductive output.

With this definition in mind, one must consider whether or not specific behavioural responses constitute coping (M, Figure 1). As mentioned above, behavioural flexibility is generally considered to represent a successful coping response, while abnormal behaviour or behavioural pathology constitutes a failure to cope (Newberry, 1995; Clark *et al.*, 1997). For example, abnormal behaviour in chimpanzees is believed to develop when responses to environmental conditions exceed the limits of the species-typical behavioural flexibility (Walsh *et al.*, 1982). However, evidence from other species suggests that individuals that exhibit abnormal behaviour in captivity may have improved reproductive output relative to individuals which do not exhibit abnormal behaviour (Jones *et al.*, 2010), suggesting that at least some abnormal behaviour may serve as coping to captive environments. Certainly, many abnormal behaviours are clearly pathological, cause distress and constitute a coping failure (e.g. self-injurious behaviour; Reinhardt & Rossell, 2001) but there is a need to determine whether abnormal behaviour is necessarily pathological.

It is likely that many 'abnormal' behaviour patterns are labelled as such because they appear abnormal from an anthropocentric perspective, or are not exhibited as frequently in nature (Birkett & Newton-Fisher, 2011). However, these criteria do not necessarily mean that the behaviour is pathological. Davison *et al*. (2004) define pathology as anatomical, physiological or psychological deviations from the norm resulting from disease or disorder. Wakefield (1992) proposes that human psychopathology should be considered in terms of harmful dysfunctions: as both causing distress and impeding functioning. Similarly, I suggest that behaviour in animals should be assessed accordingly; behavioural pathology should be considered as a state of being which causes an individual distress or impedes biological functioning. Thus, unless an abnormal behaviour impedes biological functioning or causes distress to an animal, it is not pathological.

For this reason I suggest that behavioural responses of captive animals to stress lie somewhere along a continuum of coping whereby flexibility and plastic behavioural responses lead to good well-being and ultimately survival and reproductive success (Newberry, 1995; N, Figure 1). On the opposite end of the continuum, true pathology results in poor well-being and eventually reduced reproductive output or premature death (O, Figure 1). Both good well-being resulting from flexibility and compromised well-being resulting

from pathology are likely to generate reinforcement on the response exhibited (P, Figure 1), but how strongly these feedback effects influence future responses to stress remains to be tested.

Where the responses of the chimpanzees in my studies fall along this continuum is not clear. On the one hand, the results of Chapter 2 with regard to crowding suggest that, as aggression did not escalate, the chimpanzees exhibited flexibility and successfully coped with the stress of spatial restriction. The social changes described in Chapter 4 resulted in a similar pattern of flexible responses and limited aggression, again suggesting successful coping. However, the space use and group spacing of the chimpanzees in the new enclosure may indicate that the stress of the previous, spatially limited environment resulted in a failure to cope. While the space use and spacing patterns of the chimpanzees are abnormal in the sense that free-living populations do not display such limited spacing (Jane Goodall, Pers. Comm.), whether the space use described is pathological, and therefore compromises well-being, is moot. If the self-imposed limitations on space use and group spacing are not affecting the well-being of the chimpanzees then they have coped successfully. However, if efficient space use implies good well-being, then the chimpanzees have failed to cope with past spatial restriction. The effects of LH manifest as cognitive deficits (Maier & Seligman, 1976; Maier, 1980), impeding normal cognitive functioning. Thus, I believe that the spatial behaviour of the chimpanzees constitutes a form of pathology which is not necessarily distressing to the chimpanzees, but impedes normal biological functioning.

While the model I propose (Figure 1) is by no means all-encompassing, it expands on the existing framework and attempts to incorporate various possibly overlooked factors that can contribute to understanding the responses of captive animals to stress. My model of the stress response is very linear but these effects are likely to interact in very complex, additive or multiplicative ways. While my model is based on my findings, relating specifically to chimpanzees, it could apply to other captive primates.

Implications and future directions

Unfortunately, due to the nature of my studies, factors such as cultural, neurological, cognitive and personality effects could not be investigated for the chimpanzees at the Johannesburg Zoo but various aspects of the model presented above require further enquiry. For example, with the exception of one study that I am aware of (Hook *et al.*, 2002), how

cultural transmission may drive behavioural expression of chimpanzees in captivity remains unexplored. The role of cognition in mediating chimpanzee responses to stress is also an important area of interest that requires investigation. In addition, many aspects of chimpanzee biology make them unique subjects for this area of study, but how generalisable the outcomes of my studies are to other species is uncertain.

The actual motivational thresholds involved in the responses of chimpanzees to environmentally imposed stress are also of interest. For example, at what point does a chimpanzee opt for one behavioural tactic over another? What are the factors underpinning the decision to adopt a tension-reduction or conflict-avoidance response in response to spatial crowding? These ideas may be difficult to investigate, but may also prove crucial to our further understanding of how chimpanzees respond to the stressors of captivity.

The findings of my study have important implications for the practical aspects of captive chimpanzee maintenance but highlight many theoretical concerns as well. Echoing suggestions by other authors (Ross & Lukas, 2006), the results of my study provide evidence that careful planning and assessment is needed when designing captive environments as the provision of appropriate space is essential for good animal well-being (Stricklin *et al.*, 1995). There is a need to examine the process of reconstruction of enclosures at all stages, bearing in mind the effects of spatial restriction on captive chimpanzees prior to, during and both immediately after and in the long-term following enclosure change. The appropriateness of the enclosure must also be given careful consideration, as species biology and past experience should determine the size, structure and composition of the space provided to animals within the constraints of available space and finances. Enclosures should be designed with both functional and aesthetic elements to ensure that the new space is used appropriately, but still provides for the needs of zoo visitors.

The emergence of abnormal behaviour as a potential outlet of crowding stress in my study suggests that perhaps the effects of crowding and responses to spatial restriction are not necessarily as clearly understood as originally thought. In addition, the inconsistencies between the outcomes for crowding and the associated roles of social cohesion, crowding duration and individual-based effects suggest that more work on the topic is needed. The outcomes of such studies would be of both practical and theoretical importance (de Waal, 1989).

Behavioural flexibility has emerged from my study as an important aspect of individual functioning for captive chimpanzees in captivity. The flexible responses of individuals in my study provided a mechanism for coping with the spatial and social stressors

imposed on them by the zoo environment. However, the degree to which this flexibility derives from cognitive or innate species-typical effects remains to be tested. A lack of environmental stimulation is known to have various negative effects on animals (e.g. Würbel, 2001) but how unstimulating environments might influence behavioural plasticity requires further investigation. Moreover, whether behavioural flexibility may afford chimpanzees a degree of resilience to stress requires further examination.

Not only have my study outcomes highlighted the importance of behavioural plasticity but have also shown how an inability to respond in a flexible manner can generate abnormal behavioural responses. The importance of the SCD effects described in Chapter 3 extends beyond the scope of animal welfare and the stress response. Many enrichment-based studies have described treatments comparing animals moved from or housed in small barren enclosures to large enriched enclosures. Rearing subjects under impoverished conditions may bias the outcomes of studies (Würbel, 2001) and based on my results, it appears that spatial restriction may have similar effects. Whether the pattern observed in my study reflects a true cognitive deficit has to be tested and future work should focus on the ontogeny of spatial perception. Current work suggests that SCD effects are emergent in a variety of taxa (D'Egidio, in prep.), suggesting that SCD effects manifest irrespective of brain complexity and intelligence but the degree to which SCD may interfere with normal spatial perception and as such, influence experimental outcomes, is unknown. If the effects observed in my study really reflect a cognitive deficit, specific test protocols may also be affected. For example, measuring anxiety in an open-field test (e.g. Carvajal *et al.*, 2009) with animals that display SCD effects may generate anomalous or biased estimates of anxiety.

SCD effects may also influence conservation. Chimpanzees can be successfully reintroduced into nature given specific conditions (Goossens *et al.*, 2005) but they are notoriously difficult to integrate into natural free-living populations (Treves & Naughton-Treves, 1997; Goossens *et al.*, 2005; Farmer *et al.*, 2006). Given their endangered status, factors which may hinder reintroduction efforts must be minimized to ensure successful reintroduction. Preliminary studies from rehabilitated and released Vervet monkeys *Chlorocebus aethiops* (formerly *Cercopithecus aethiops*) suggests that post-release spacing of individuals may be influenced by past spatial experience, including space use in the immediate vicinity of the release cage of the monkeys as well as tight inter-individual spacing during daily activities post-release, remarkably similar to the chimpanzees in my study (Bratt, 2010).

However, one aspect of SCD requires further investigation to determine the influence of SCD effects on conservation and reintroduction programs. The longevity of SCD effects must be quantified. My study was conducted almost five years after the change of enclosure took place, suggesting that SCD effects may persist for long time periods. However, just how long SCD effects can persist must still be studied. Work on learned helplessness in dogs suggests that the effect is not necessarily permanent, and can be ameliorated (Seligman *et al.*, 1968). It is possible that the longevity of SCD effects is dependent on the time of exposure to the stimulus, much in the same way that the duration of exposure to environmental enrichment determines how long the effects last in mice (Amaral *et al.*, 2008) or that SCD effects may be perpetuated through cultural transmission, but these effects require substantial investigation.

Conclusion

My thesis is best considered as a series of case-studies, akin to those used in human psychological research, exploring how the environmental stressors of captivity influence the behaviour of captive chimpanzees. I utilized the changes imposed upon the chimpanzees at the Johannesburg Zoo to examine their general responses and concomitant welfare issues. There is a need to replicate my studies and compare the outcomes in other studies. However, due to the nature of the imposed spatial, social and environmental changes, true replication may prove difficult to achieve, particularly since the responses by the chimpanzees are nuanced by individual differences, histories and group composition. Individual variation and variation between groups is likely to generate different outcomes to similar changes in space and sociality, but the studies presented here provide a framework against which future studies can be compared. However, given the clear significance of my findings for animal welfare and well-being, it is important that the ideas and hypotheses generated be tested further in chimpanzees particularly and primates generally.

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Appendix Chapter. Volunteer experience influences the conclusions of behavioural experiments

Abstract

Volunteers offer an inexpensive and rapid means of collecting behavioural data, but their reliability is often overlooked. Past research has suggested that observers that were inexperienced are equally adept at recording behaviour as experienced observers, and inexperience was regarded as being merely unfamiliar with a sampling technique but not unknowledgeable about behaviour. The aims of our study were (i) to investigate the reliability of relatively naïve volunteers (i.e. those with no prior behavioural scoring experience) as behavioural data collectors; and (ii) to test the influence of the strength of inter-observer concordance on the outcome of testing a specific ethological hypothesis. Two cohorts of volunteers (high school and university students) conducted observations on a group of captive chimpanzees, simultaneously with an experienced observer (myself), recording behaviour and the location of the chimpanzees in their enclosure. Kendall's Tau agreement scores and odds ratios indicated poor agreement between inexperienced volunteers and the experienced observer, regardless of the educational experience of the volunteers and difficulty of the behaviour scored. We compared the data between the volunteers and experienced observer by independently testing each dataset with regard to the hypothesis that the chimpanzees were stressed by being in close proximity to the public. The school cohort data supported the hypothesis, while the time-matched experienced observer data suggested no relationship between public proximity and stress in chimpanzees. A separate analysis of the university cohort and time-matched experienced observer data both indicated that chimpanzees were more stressed at locations away from the public. These findings suggest that inter-observer agreement scores offer insights into the precision of data but not accuracy. Furthermore, the use of volunteers as data collectors should be assessed in relation to the aims of the study in question, since volunteers may be appropriate for studies of general patterns but not for detailed ethological examinations.

Introduction

Ethology assumes that behaviour recorded by observers reflects behaviour performed by animals (Coelho & Bramblett, 1981). Consistency in data collection is particularly important when datasets are compiled over a long timeframe (Coelho & Bramblett, 1981), when data are used for complex and detailed analyses (Jones *et al.*, 2001) or when ratings or recordings of behaviour encompass comparatively subjective measures, such as animal welfare (Meagher, 2009) or personality (Scott *et al.*, 2009). Biased or unreliable recording of behaviour decreases both accuracy and precision of data and thus compromises the scientific integrity of a study.

One way to ensure accuracy and precision of the data gathered by observers is to compare human observers against an absolute measure of behaviour. For example, O'Driscoll *et al.* (2008) compared the recordings of human observers of the lying behaviour of cattle against an automated data logging system and found that agreement between the two systems was high. However, data loggers are not feasible for all behaviours. For example, domestic cats *Felis catus* adopt a sedentary posture for grooming, engaging in bites, licks or scratches (Trulson, 1976), behaviours which a data logger might record as lying or resting. Furthermore, behaviour is often defined both qualitatively and quantitatively. A mouse moving through an enclosure in a circuit may not be abnormal unless it is performed repeatedly which may be considered stereotypic (Jones *et al.*, 2008). Therefore, behaviour recording requires that observers use a certain amount of subjective judgement in order to accurately record behaviour.

Given the complex and subtle nature of behaviour, many studies compare records between multiple observers as a means of assessing inter-observer reliability (Jones *et al.*, 2001). Most studies have shown good inter-observer agreement with a variety of methodologies ranging from ethogram-based continuous sampling (Coelho & Bramblett, 1981) to subjective assessment of acute pain experience in lambs (Molony *et al.*, 2002). In addition, observer agreement ratings do not appear to decay (Coelho & Bramblett, 1981).

There is some debate as to the role of experience in observer reliability. Some suggest naïve individuals may make better observers as they are less likely to be biased (Meagher, 2009) and may provide novel insights that trained ethologists might overlook (Shyan-Norwalt, 2005; Tami & Gallagher, 2009). Others argue that experienced observers make more accurate observations due to their familiarity with the methodology and/or study subjects (Margulis & Westhus, 2008). Also, individuals that regularly engage with animals

are more likely to achieve good agreement than individuals with no experience of the subjects in question (Lloyd *et al.*, 2007).

Despite the importance placed on observer experience, studies have found that inexperienced individuals are as good as experienced individuals in scoring behaviour (Coelho & Bramblett, 1981; Wemelsfelder *et al.*, 2000; Jones *et al.*, 2001). However, these outcomes should be interpreted with caution as Coelho & Bramblett (1981) had the observers undergo formal study of primate ethology and extensive training prior to beginning observations. Furthermore, both the studies of Wemelsfelder *et al.* (2000) and Jones *et al.* (2001) utilized observers who, while lacking background in the specific scenario being tested, had extensive zoological and ethological experience, using psychology and zoology graduates and trained ethologists respectively. Therefore the term 'inexperienced' is misleading and thus we hereafter consider inexperienced individuals as having no experience with behavioural data collection or training in zoology, psychology or ethology.

Many zoo-based studies use volunteer data collection (Newman *et al.*, 2003; Shyan-Norwalt, 2005; Margulis & Westhus, 2008) because rigorous behavioural observation is often impractical for staff (Margulis & Westhus, 2008). However, in general, volunteers typically have a variety of skill sets and experience levels (Arbon *et al.*, 2006) and thus may misinterpret instructions (Jones *et al.*, 2001), find behaviours difficult to identify (Tami & Gallagher, 2009) or require a degree of training to maintain accuracy (Molony *et al.*, 2002).

To date, no empirical investigation into the reliability of zoo volunteers has been conducted. The first aim of my study was to assess the reliability of inexperienced volunteers as data collectors in a zoo setting with regard to education and experience effects on volunteer efficacy. As experience level appears to have little influence on inter-observer agreement (Coelho & Bramblett, 1981; Wemelsfelder *et al.*, 2000; Jones *et al.*, 2001; Tami & Gallagher, 2009), I predicted that data collected by inexperienced volunteers and those collected by an experienced individual (myself) would generate good inter-observer agreement scores. Age and aptitude do not influence the ability of volunteers to conduct wildlife surveys (Newman *et al.*, 2003) and thus, I predicted that the level of education of inexperienced volunteers would have no influence on inter-observer agreement scores. Finally, as some behaviours may be more difficult to recognise than others (Tami & Gallagher, 2009), I predicted that agreement would be better for easily identifiable behaviours than for more difficult behaviours.

There are various standardized statistical measures of inter-observer agreement, including Spearman's correlation coefficient (O'Driscoll *et al.*, 2008), Cohen's Kappa

coefficient (Rousing *et al.*, 2005), Kendall's coefficient of concordance and effective percentage agreement (Jones *et al.*, 2001). No distinct cut-off rule exists for the interpretation of these agreement estimates, but scores of 0.7 or more are generally considered to represent acceptable agreement between observers (Meagher, 2009) but some studies have considered agreement scores as low as 0.5, effectively representing an approximate 50% agreement (Bolig *et al.*, 1992; Wielebnowski, 1999). In contrast, hypothesis testing typically requires a significance level of 95% in order to reject the null hypothesis. Data from several observers at only a 50% agreement may introduce noise into a dataset, creating a bias that may compromise the outcomes of hypothesis testing. This presents a troubling question: does inter-observer agreement, or a lack thereof, influence the outcome of hypothesis testing?

Thus, the second aim of my study was to determine whether agreement scores influence the outcome of hypothesis testing. For this study, all observations by both the experienced observer and all volunteers were conducted with a group of captive chimpanzee study subjects, recording behaviour and location within the enclosure. Some suggest that primates are stressed by public interactions (Chamove *et al.*, 1988), and thus I predicted that the chimpanzees would engage in more anxiety-related behaviours (self-directed grooming, abnormal behaviour and vigilance) in locations within their enclosures that place them into close proximity with or unsheltered from the public compared to locations further from or less exposed to the public. Conversely, when away from the public, the chimpanzees would engage in "relaxation" behaviours (social grooming, social play, resting). I assessed this prediction by analysing data collected by the inexperienced volunteer observers and time-matched (data collected simultaneously on the same chimpanzees) experienced observer data to ascertain whether the conclusions differ depending on which observers collected the data.

Materials and Methods

Zoo volunteers

This study was conducted at the Johannesburg Zoo, South Africa, from August 2006 to October 2008, and formed part of the Jane Goodall Institute South Africa's ChimpanZoo research programme. A mixed sex and age group of 32 volunteers was recruited from the University of the Witwatersrand and various Johannesburg schools, including Beaulieu College, Redham House High School and Northcliff High School. Volunteers ranged from approximately 12 to 24 years of age and represented various cultural and economic

backgrounds. None of the volunteers had any prior experience in behaviour observation or behaviour recording or had studied animal behaviour. Of the 32 volunteers recruited, 19 female volunteers participated consistently (> 3 observation sessions) and were used in this study.

Animal subjects and husbandry

The subjects observed by the volunteers were a stable mixed-composition group of captive chimpanzees housed socially at the zoo. The group comprised four males and five females ranging in age from newborn infants to adults of 24 years (L.Duncan, unpublished; Chapter 3). The chimpanzees were housed in a large indoor-outdoor naturalistic exhibit with the outdoor enclosure (± 2500m^2) divided into two sections by a wall with an open doorway linking the two (Figure 1). All the surrounding walls were 8m high and capped with electric fencing. Each enclosure section had 4-5m wide moats, bordered by 1.5m high electric fencing and 30cm high electric fencing extending out of the water approximately 2m into the moat, separating the enclosure from the public viewing areas. One of the enclosure sections had large, reinforced-glass viewing windows through which the public could observe and interact with the chimpanzees.

Both sections comprised a variety of trees, shrubs, grasses, rocks and logs and provided *ad libitum* access to water. The chimpanzees were fed a mixture of fresh fruit and vegetables, primate pellets and boiled eggs twice daily; feed was scattered randomly throughout the outdoor sections at 10h00, to encourage the chimpanzees to leave the night rooms, and throughout the night rooms at 15h00 on weekdays (16h00 on weekends) to encourage the chimpanzees to enter the night rooms.

Volunteer training and observation procedures

Prior to any structured observations, volunteers received a 30 min talk on the study of behaviour and its impact on animal welfare, followed by a 30 min talk on the observation procedure, including a simple but detailed explanation of the sampling method used, and the requirements of volunteers. Following the talk, volunteers were taken to the chimpanzee exhibit, where a system of zones, based on proximity to the public (Figure 1), was explained to them with the aid of diagrams of the enclosure. The volunteers and I then conducted a single 30 min ‘practice’ observation session, according to the observation protocol described

below, followed by a brief discussion session to clarify any potential points of confusion. The records of the practice session were not collected or used in later analysis.

Thereafter, observations were conducted on days and at times that suited volunteers. Observation sessions were carried out between 10h00 and 15h00 on weekdays and 10h00 and 16h00 at weekends. Instantaneous focal sampling (Martin & Bateson, 1986) at 30 sec intervals for 30 min was used. Observers recorded the behaviour (Table 1) and location, scored as zones occupied by the focal individual (Figure 1), simultaneously such that each 30 min session provided 60 simultaneous behaviour and location frequency scores. Volunteers were instructed to record the behaviour being conducted at a given time. I served as the experienced observer and was present at all sessions, recording behaviour and locations for the same focal chimpanzee according to the same protocol simultaneously with volunteers. No comparison or copying of data was permitted between volunteers or between volunteers and I during or following observation sessions. The volunteers and I remained in close proximity at all times and I marked time for all scorers every 30 seconds using a digital stopwatch. Volunteers and I used identical datasheets. Following the completion of each session, we collected the datasheets and made copies of the sheets for later analysis, returning the sheets to the volunteers at the next session, as mandated by the Jane Goodall Institute South Africa.

Data analysis

Volunteers participated in a total of 70.5 h of data collecting (mean per volunteer: 3.7 hrs). The data were separated into two cohorts based on the level of education of the volunteers. Volunteers still in school were classified as the ‘school’ cohort (approximately 12-16 years old) while volunteers at university were classified as the ‘university’ cohort (19-24 years old).

In order to investigate whether the ease with which behaviours were recognised influenced recording, three ‘easy’ behaviours and three ‘difficult’ behaviours were selected from the ethogram and analysed. The three easy behaviours, travel, forage and inactivity, were common to most animals. The three difficult behaviours were two forms of play, object and locomotor play (play is often ambiguous and an inexperienced individual might easily mistake object manipulation or certain locomotion, such as climbing, for play) and vigilance (vigilance is typically brief and rapid and is thus likely to be overlooked).

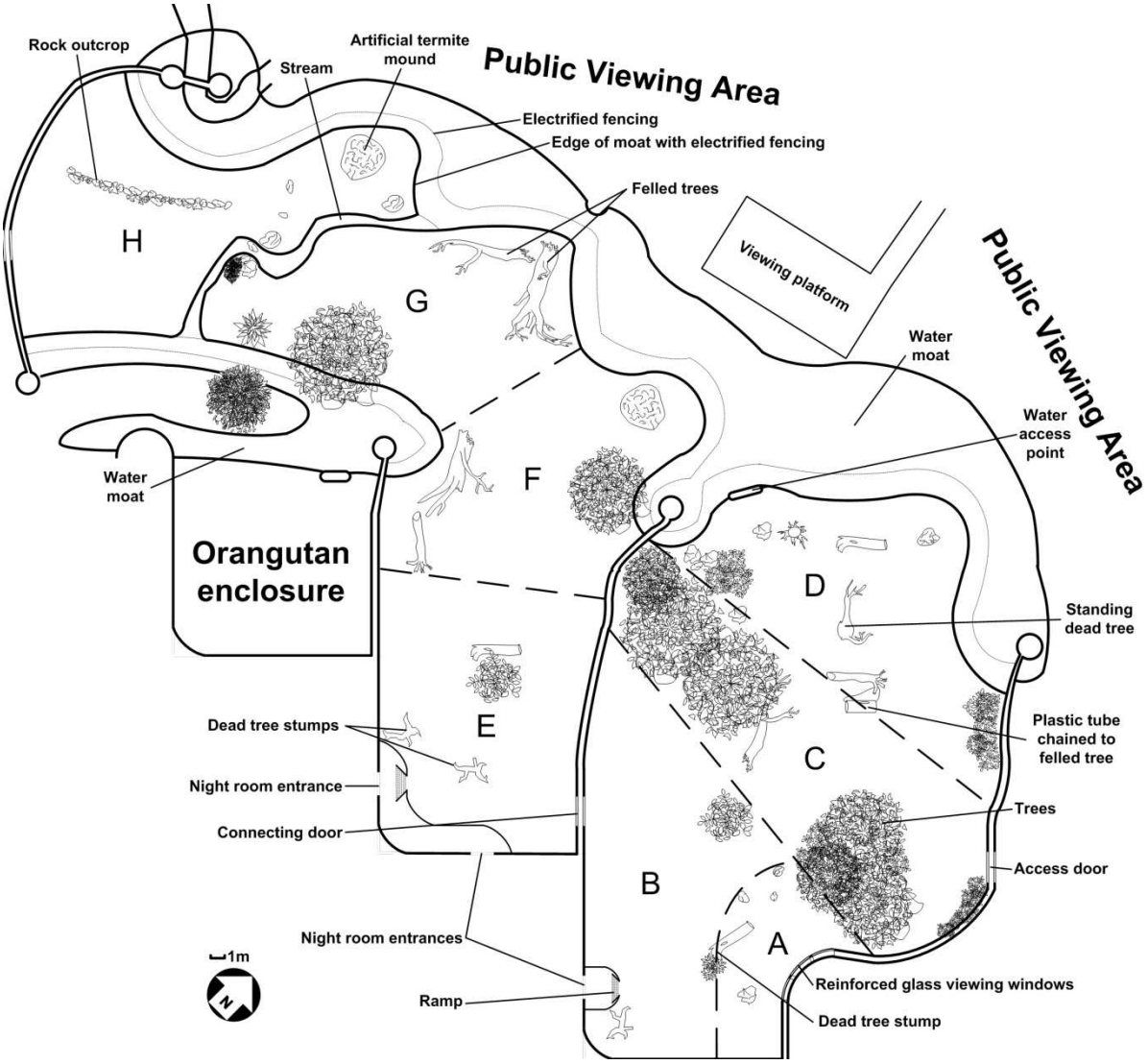

Figure 1. Outdoor housing area of the chimpanzee exhibit at the Johannesburg Zoo Ape House, South Africa, drawn to scale. Dashed lines denote the boundaries of zones, based on proximity to the public. Zones A-H are labelled with corresponding letters.

For each session, the specific easy and difficult behaviours were compared between each volunteer and my own data using Kendall's tau (τ :after Lloyd *et al.*, 2007). A cohort-specific τ agreement score was calculated for each cohort per behaviour as well as the coefficient of variance. Both cohorts were also pooled and compared using the τ agreement score. Similarly, the zone utilization records for each session were compared between my records and volunteer records, for each cohort and for both cohorts together. As cohorts did not necessarily conduct observations at the same time, no direct comparison between the two cohorts was made. Agreement scores were considered as acceptable for $\tau \geq 0.7$ (Meagher, 2009).

Table 1. Definitions of behaviours observed in the chimpanzee groups at the Johannesburg Zoo, South Africa, used by inexperienced volunteers and an experienced observer to assess the reliability of volunteer data

Behaviour	***Definition***
Travelling	Movement from one location to another, not obviously searching for food. Included walking, running and climbing
Foraging	Searching for, manipulating or consuming food or drink.
Vigilance	When the chimpanzees ceased other activities in order to monitor or observe their surroundings or other individuals
Inactive	Resting, either standing, sitting or lying down. Included sleeping
Abnormal	Coprophagia/urophagia, self-mutilation, faeces throwing and hair plucking. Other behaviours were scored as abnormal based on the context in which they occurred and whether they occurred repetitively (>3 times in succession; Jones *et al.*, 2008). These included nipple pulling, abnormal gait and posturing and chronic masturbation
Aggression	Chasing aggressively (characterised by sneering, open and closed grins and compressed lip faces. Usually associated with screams, barks and 'wraaa' calls; Goodall, 1986) or fighting with one another. Included aggressive gesturing or signalling
Social play	Wrestling, playful biting and playful chasing (characterised by a relaxed face, possibly with a drooping lower lip, or a full play face. Usually silent but may include soft grunts or hoots; Goodall, 1986)
Object play	Play directed at or involving an inanimate object
Locomotor play	Solitary active play. Included running, rolling, swinging or somersaulting
Self-grooming	Licking, cleaning, picking at and removing items from their own skin or hair. Included self-scratching
Social grooming	When individuals engage in licking, cleaning, scratching, picking at or removing items from the skin or hair of other chimpanzees
Other	Any identifiable behaviour that did not obviously fit into the other behaviour categories
Hidden	Chimpanzees were obscured from view or behaviour was unidentifiable according to the other categories listed

Odds ratios are frequently used in epidemiological research to assess diagnostic test performance, as they provide a measure of the strength of association between a medical treatment and a resultant outcome (Glas *et al.*, 2003). The ratio ranges between zero and infinity, whereby a value of 1 suggests no discrimination between treated and untreated patients, while values lower than 1 suggest improper test interpretation and values higher than 1 suggest increasing test discrimination performance (Glas *et al.*, 2003). By applying odds ratios to inter-observer agreement, we were able to generate a measure of agreement since odds ratios provide an estimation of whether a volunteer under- or over-estimated a particular behavioural parameter. In this case, a value of 1 would suggest perfect agreement (no discrimination) between observers while lower values and higher values would suggest that the inexperienced observer in question under- and over-estimated the behaviour respectively

in relation to an experienced observer. Thus, the following modified odds ratio calculation was used as an estimate of inter-observer agreement and bias:

$$Observer\ Odds\ ratio = \frac{A/a}{B/b} = \frac{A \times b}{B \times a}$$

where *A* and *B* refer to the number of times a behaviour was scored by observers A and B respectively and *a* and *b* refers to the number of times a behaviour was not scored by observers A and B respectively. Odds ratios were calculated to compare the data from each volunteer to my own time-matched data.

Next, to establish where potential differences might lie between τ agreement scores for the two cohorts and between easy and difficult behaviours, cohort τ scores were compared between cohorts and easy and difficult behaviours. To assess whether education influences behaviour scoring, a Mann-Whitney U test was used to compare the agreement scores of both the school and university cohorts. Agreement scores between easy and difficult behaviours were compared using a Wilcoxon matched pairs test.

In order to assess the reliability of volunteer data collection with regard to hypothesis testing, enclosure zones were labelled as high- or low-risk, according to how exposed or close chimpanzees in these zones were to zoo visitors. The high-risk zones were A, D, G and H while the low-risk zones were B, C, E and F (Figure 1). All the high- and low-risk zone data were combined into two categories, 'high-risk' and 'low-risk' respectively. At no point during data collection were volunteers aware of the hypothesis to be tested, nor the significance of the zonation used.

Behaviour such as vigilance, self-directed grooming (Carder & Semple, 2008) and abnormal behaviour (Fox, 1984) appear to be indicative of stress, while behaviours like social play (Tacconi & Palagi, 2009) and social grooming (Dunbar, 2010) serve relaxation and social bonding functions in primates. Thus, data for anxiety-related (vigilance, abnormal and self-grooming) and relaxation behaviours (inactive, social play and social grooming) were pooled into two categories respectively: Anxiety and Relaxation. I then conducted four separate two-tailed generalized linear models (GLZ) with logit link functions and a binomial error structure using Statistica 8.0 (StatSoft, 2008); the GLZs tested the school cohort, university cohort or my time-matched data for the school cohort and my time-matched university cohort data. This allowed us to generate four sets of independent model outcomes for the same hypothesis based on the four datasets. Model significance level was set at $p \leq$

0.05 and significant differences for interaction effects were identified through β-estimates and confidence intervals. Because the two behaviour categories were mutually exclusive (the behaviours examined were either anxiety- or relaxation-related and could not be classified as both), the counts of each category were tallied as a binomial absence/presence structure. Zone-risk (high-risk or low-risk) and behaviour (anxiety or relaxation) were used as categorical predictor variables and the binomial absence/presence structure of counts was used as the dependent response variable.

Results

Inter-observer agreement

All Kendall's Tau (τ) scores and ranges of observer odds ratio are presented in Table 2. The mean τ agreement score for all behaviours based on the total pooled scores did not reach acceptable agreement ($\tau = 0.58$). Neither easy ($\tau = 0.64$) nor difficult behaviours ($\tau = 0.51$) reached acceptable agreement, based on total pooled scores. For the pooled data (Table 2: Total Pooled) for the easy behaviours (travel, forage and inactive), only travel achieved good τ agreement between volunteers and the experienced observer. For the difficult behaviours (vigilance, object play and locomotor play), only locomotor play achieved good τ agreement. Agreement between zones scored by volunteers and the experienced observer achieved acceptable τ agreement for the school ($\tau = 0.89$; CV = 0.07) and university ($\tau = 0.85$; CV = 0.09) cohorts, as well as for both cohorts pooled ($\tau = 0.87$).

For the school cohort, the range of observer odds ratios (ODD) was lowest for the difficult behaviours (0.08 – 3.03; mean = 1.32) and larger for the easy behaviours (0.02 – 16.28; mean = 1.20). The university cohort exhibited the opposite pattern, with the lowest range for the easy behaviours (0.04 – 2.98; mean = 0.88) and the largest range for the difficult behaviours (0.05 – 3.90; mean = 1.49). Travel behaviour generated the lowest ODD for both cohorts. The largest range of ODD's was found for resting behaviour for the school cohort and object play for the university cohort.

Cohort and behaviour differences

The τ agreement scores were not significantly different between the school and university cohorts ($U = 17.5$: $p = 0.936$). Similarly, no significant differences were found between the easy and hard behaviour τ scores ($Z = 0.105$: $p = 0.917$).

Table 2. Kendall's Tau (τ) statistics with coefficient of variance (CV) and ranges of observer odds ratios (ODD) calculated for comparison of inter-observer agreement scores for three 'easy' behaviours and three 'difficult' behaviours (based on ease of identification) scored by two cohorts of inexperienced volunteers and an experienced observer at the Johannesburg Zoo, South Africa. Scores that achieved acceptable agreement are in bold within grey cells

			Kendall's Tau (τ) Statistic			
	Factor	Observer Cohort	CV	Cohort Score	ODD	Total Pooled (All Volunteers)
'Easy'	*Travel*	School	0.15	**0.82**	0.80 - 1.04	**0.82**
		University	0.21	**0.79**	0.82 - 1.29	
	Forage	School	0.61	0.51	0.29 - 1.08	0.54
		University	0.34	0.57	0.26 - 1.36	
	Rest	School	0.46	0.51	0.02 - 16.28	0.57
		University	0.08	0.60	0.04 - 2.98	
'Difficult'	*Vigilance*	School	1.03	0.11	0.44 - 2.63	0.11
		University	1.10	0.12	0.80 - 2.75	
	Object Play	School	0.42	0.66	0.33 - 3.03	0.65
		University	0.13	0.65	0.33 - 3.90	
	Locomotor Play	School	0.70	**0.79**	0.08 - 1.46	**0.76**
		University	0.53	**0.71**	0.05 - 1.61	

Hypothesis testing

School cohort dataset

For the GLZ analysis based on the data collected by the school cohort, behaviour (Wald $\chi^2_1 = 942.14$, $p < 0.001$) and a zone-risk*behaviour interaction effect (Wald $\chi^2_1 = 24.16$, $p < 0.001$) were identified as good predictors of the model outcomes. Zone-risk (Wald $\chi^2_1 = 3.78$, $p = 0.054$) was not a good predictor of the model outcomes. The zone-risk*behaviour interaction effect (Figure 2a) showed significantly greater relaxation behaviour in high- than in low-risk zones while anxiety behaviour was found to be significantly greater in low- than high-risk zones.

School cohort time-matched experienced observer dataset

The GLZ analysis using the time-matched experienced observer data identified zone-risk (Wald $\chi^2_1 = 10.95$, $p < 0.001$) and behaviour (Wald $\chi^2_1 = 316.12$, $p < 0.001$) as good predictors of the model outcomes. The zone-risk*behaviour interaction (Wald $\chi^2_1 < 0.001$, $p = 0.993$; Figure 2b) was not a good predictor of the model outcomes.

University cohort dataset

Zone-risk (Wald $\chi^2_1 = 81.61$, $p < 0.001$), behaviour (Wald $\chi^2_1 = 833.02$, $p < 0.001$) and a zone-risk*behaviour interaction effect (Wald $\chi^2_1 = 37.62$, $p < 0.001$) were identified as good predictors of the model outcomes. The interaction effect (Figure 2c) showed significantly greater relaxation behaviour in high- than low-risk zones and significantly greater anxiety behaviour in low- than high-risk zones.

University cohort time-matched experienced observer dataset

The time-matched experienced observer dataset GLZ analysis identified zone-risk (Wald $\chi^2_1 = 77.28$, $p < 0.001$), behaviour (Wald $\chi^2_1 = 389.22$, $p < 0.001$) and a zone-risk*behaviour interaction effect (Wald $\chi^2_1 = 11.51$, $p < 0.001$) as good predictors of the model outcomes. Significantly greater relaxation behaviour in high- than low-risk zones and significantly greater anxiety behaviour in low- than high-risk zones were found for the zone-risk*behaviour interaction effect (Figure 2d).

Discussion

This study aimed to determine the reliability of a high school cohort and university cohort of volunteers with no previous experience in zoology, psychology or ethology, as data collectors in a behavioural experiment on chimpanzees. Two approaches were used to assess reliability: inter-observer agreement, to compare data from inexperienced volunteers against time-matched data from an experienced observer, and a comparison of the outcomes of testing the hypothesis that chimpanzees are stressed by close proximity to zoo visitors between the respective data collectors (volunteers and an experienced observer).

There was acceptable agreement between inexperienced volunteers and the experienced observer for only two (one easy behaviour, one difficult behaviour) of the six behaviours tested for the high school and university cohorts separately and when the data were pooled. These findings contradict my initial prediction and the literature, because experience is generally held to have little influence on inter-observer agreement (Coelho & Bramblett, 1981; Wemelsfelder *et al.*, 2000) and inexperienced observers have been shown to achieve acceptable agreement with experienced observers in scoring sonograms (Jones *et al.*, 2001) and identifying and recording dog behaviour (Tami & Gallagher, 2009).

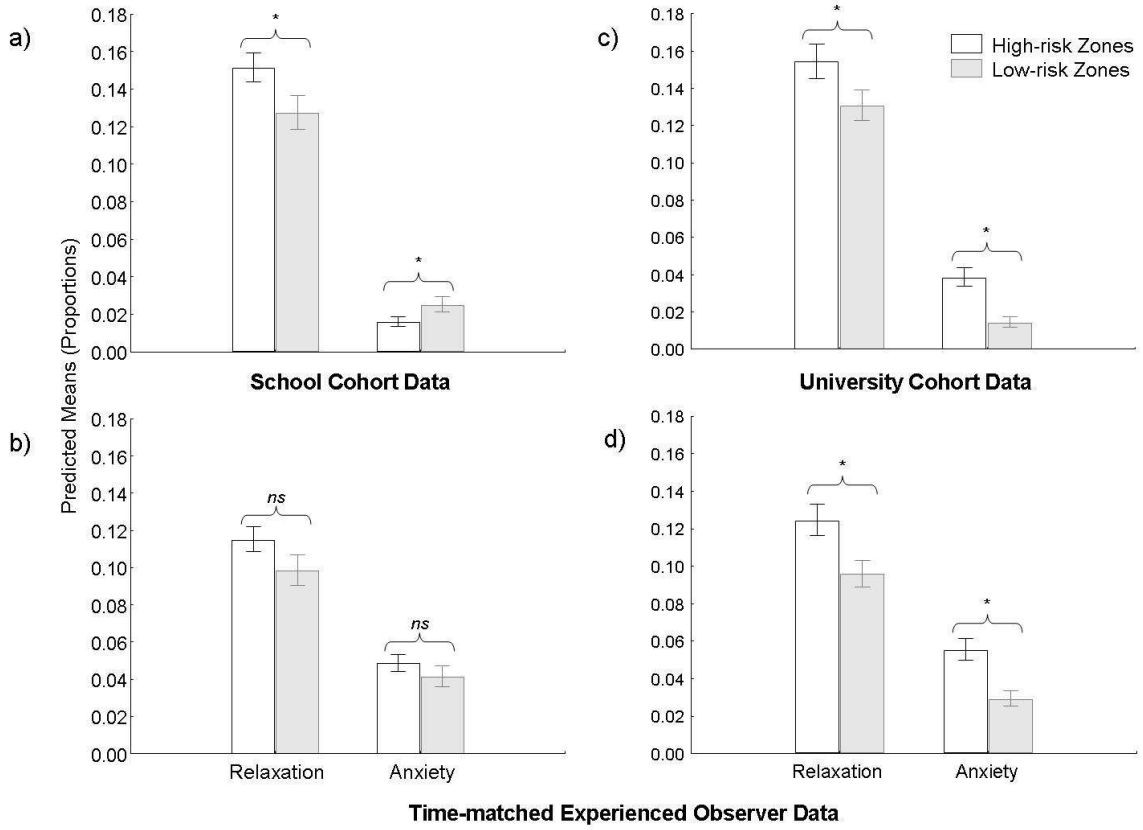

Figure 2. Predicted means data for Zone-risk*Behaviour interaction effects from four separate generalized linear model analyses carried out on four datasets. Datasets were collected by two different cohorts of inexperienced volunteer observers: a) School cohort; c) University cohort. Simultaneously with the b) school cohort and d) university cohort, data were collected by a single experienced observer (myself). Analyses sought to test whether location within the enclosure (High-risk zones: areas that place the chimpanzees in close proximity to zoo visitors; Low-risk zones: areas that place chimpanzees far from zoo visitors) of the chimpanzee exhibit of the Johannesburg Zoo, South Africa, predicts the levels of relaxation-related and anxiety-related behaviours. Symbols above the bars denote significant differences (*ns* = $p > 0.05$; * = $p < 0.05$)

However, many studies that have explicitly tested and reported good inter-observer agreement between inexperienced and experienced observers have utilized inexperienced observers with a background in ethology, zoology or psychology (Wemelsfelder *et al.*, 2000; Jones *et al.*, 2001) or have enforced rigorous training on observers prior to observation sessions (Coelho & Bramblett, 1981). Thus, perhaps appropriate training might necessitate good agreement between inexperienced and experienced observers. Alternatively, stimulus-specific learning theory suggests that task performance is related to past experience with a specific stimulus (Sohn *et al.*, 2006) and thus the skill-sets of an individual are specific to particular domains (Billing, 2007). Thus, while the two cohorts differed in their level of education, neither cohort was more or less likely to perform well as a behaviour data collector because the skills were novel and had no bearing on previously learned skills.

In contrast to most of the behaviours, agreement on which zones a chimpanzee occupied achieved the best inter-observer scores. This may be because the demarcation of zones was clearer (through the use of diagrams and fixed physical elements of the enclosures) than the distinctions between behaviours. Alternatively, given the size of the zones, perhaps volunteers scored zones more precisely as there were only 8 large zones, whereas there were 13 behaviour categories.

It has been suggested that some behaviours are easier to identify than others (Tami & Gallagher, 2009) but the findings of this study do not support this prediction. No significant difference emerged when comparing τ agreement scores for easy and difficult behaviours, suggesting that the nature of the behaviour scored has little influence on inter-observer agreement. However, it is possible that the classification as either 'easy' or 'difficult' was not correct, which is supported by the greater range of observer odds ratios for easy behaviours in the school cohort. Agreement scores for the school and university cohorts were not significantly different, suggesting that level of education had little influence on τ agreement scores between inexperienced and experienced observers. This finding supports my initial prediction and the findings of Newman *et al*. (2003) that age and aptitude had little effect on the ability of inexperienced individuals to conduct wildlife surveys.

The outcomes of the hypothesis tests suggest a more complex scenario. The data from the school cohort identified behaviour, zone-risk*behaviour but not zone-risk as good predictors of the model outcomes, with more anxiety behaviour in high-risk zones. The time-matched experienced observer data identified behaviour and zone-risk as good predictors, but not zone-risk*behaviour. Thus, we conclude that the school cohort data support the hypothesis, suggesting chimpanzees do find close proximity to the public stressful. However, the data simultaneously collected by the experienced observer suggests that there is no relationship between proximity of zoo visitors and stress behaviour of the chimpanzees. In contrast, the data of the university cohort and the time-matched experienced observer both highlighted behaviour, zone-risk and zone-risk*behaviour as good predictors of the model outcomes, both with more anxiety behaviour in low-risk zones. The conclusion of these findings suggests that close proximity to zoo visitors may not be stressful for the chimpanzees.

Curiously, the time-matched experienced observer data for the school and university cohorts respectively generated different model outcomes. The observations of the school cohort began in March 2007 and ended in July 2008, while the observations of the university cohort (with the exception on one individual who started in March 2007) started in April

2008. Thus the model outcome differences between the two experienced observer datasets may reflect variation in the behaviour of the chimpanzees as the data were collected over two different time periods.

It is possible that the school cohort, comprising early adolescents, perceived the observed behaviour in a very different manner to the experienced observer. Adults and adolescents are known to report very different perceptions of events, such as eating behaviour at meals (Boutelle *et al.*, 2001) or risk assessment of a potentially dangerous scenario (McClure-Martinez & Cohn, 1996). In an examination of the use of different behaviour recording methods, Margulis & Westhus (2008) conclude that the sampling method used should be chosen according to the aims of the study, suggesting that all methods are appropriate when assessing broad-scale patterns of behaviour, but selected methods were more appropriate for more detailed studies. Similarly, if the interest is on general patterns of behaviour, such as zone occupancy in my study, perhaps utilizing inexperienced relatively young volunteers is still acceptable. However, if the investigation is more specific, such as which behaviours are performed in particular zones, young volunteers may no longer be an acceptable means of gathering data.

The sex of the observers may have influenced the outcome of this study, as an all-female group of volunteers was compared against a single male observer. Men performed better than women when conducting wildlife surveys (Newman *et al.*, 2003) and men and women appeared to record different frequencies of behavioural events when observing the same animal (Marsh & Hanlon, 2004). However, as suggested by the work of Marsh & Hanlon (2004), sex differences in behaviour observations may be related more to frequency or number of recorded events, as opposed to broad patterns of behaviour. In this study, the university cohort data displayed the same zone patterns of behaviour as the data of the experienced observer despite the sex differences, while the absolute levels of respective behaviours were different. Based on these differences, it might be advisable to utilize a mixed-sex group of observers. However, the sex differences in perceiving and reporting behaviour may be subtle (Marsh & Hanlon, 2004) and their influence on data collection requires further investigation.

This study suggests that perhaps inter-observer τ agreement scores are not a good indication of the reliability of the data collected by volunteers. Instead, τ agreement scores reflect agreement between observers only, and should be interpreted as such. Many studies specifically discard data collected by individuals who do not obtain acceptable agreement scores prior to analysis (Lloyd *et al.*, 2007) while other studies assume that good agreement

between observers is indicative of similar data (Margulis & Westhus, 2008) combining their data for later analysis. However, these assumptions may be questionable as agreement scores between observers may also reflect variation within the dataset, and not necessarily only variation between observers (Jones *et al.*, 2001). Thus, agreement scores may not make data any more or less valid for analysis, indicating that good agreement ensures precision, but has no clear relationship to accuracy of the data collected.

In conclusion, it appears that inexperienced volunteers (without prior behavioural/psychological training) do not show good agreement with an experienced observer when scoring behaviour. The agreement scores do not appear to be affected by age or the difficulty of recognising the behaviour being scored. However, agreement scores do not necessarily provide an indication of accuracy of the data collected as data that showed poor inter-observer agreement in the case of the university cohort and my time-matched data resulted in similar conclusions drawn from analysis of the two datasets. Therefore, agreement scores should be assessed with caution when used as a decision-making tool for data collection. The use of volunteers is vital in many behavioural studies and their value cannot be overstated. However, the data required and the aims of study should be considered when evaluating whether volunteers as behavioural observers is feasible.

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