Space use following restricted space availability in two mammals and two arthropods

Chiara D'Egidio

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Declaration

I declare that this dissertation is my own unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.

(Signature of candidate)

20/ 02 /2012

(Date)

Abstract

Captive environments can provide a variety of sources of stress for animals with space limitation being one of the primary contributors. Spatial restrictions may result in psychological stress by which the memory and learning of animals can become impaired. One solution to spatial stress has been to increase the size of the enclosure for captive animals. In my dissertation, I questioned the rationale of providing increased space by investigating whether more space leads to greater use of space.

My study had 2 aims. Firstly, I tested whether the previous experience of an individual, or of a group of individuals in a small area, would influence the subsequent use of space when they were introduced into larger enclosures. I used 4 different species (chimpanzees, striped mice, woodlice and cockroaches). Secondly, I tested whether the spatial perceptions were dependent on neuronal complexity in terms of cognitive ability, i.e. is space use of a species related to neuronal complexity. Chimpanzees and striped mice were considered to have greater neuronal complexity than woodlice and cockroaches since mammals display more complex cognition compared to arthropods. The chimpanzees comprised of 8 individuals at the Johannesburg Zoo, 7 of which were transferred from a 10 m x 10 m enclosure, in which they were housed for 2 (second youngest individual) to 25 years (oldest chimpanzee), to a 2500 m^2 enclosure (in which the youngest chimpanzee was born), and their space use was evaluated in terms of subgroup space use in the enlarged enclosure. Chimpanzees are naturally social and thus I examined group instead of individual spacing. Chimpanzee subgroups, which comprised 2 or more chimpanzees, consistently restricted their space use in the enlarged enclosure to the size of their old enclosure, choosing their positions within the enclosure based on the presence of shade availability. Striped mouse space use was evaluated in terms of individual space use because striped mice from the mesic grasslands of South Africa are solitary living. Individual striped mice were placed into an enlarged arena (200 cm x 15 cm x 100 cm; L x H x B) after being restricted in a smaller cage (36.5 cm x 20.5 cm x 15 cm) for 60 days and their space use and distance travelled were measured against the area of their old housing. The space use of restricted striped mice was evaluated against a control group. The striped mice from the restricted group restricted their space use to the size of their original housing, with those having a shy personality showing more restricted space use than bold individuals. Woodlouse and cockroach space use was evaluated in same sex pairs, as woodlice and cockroaches tend to form aggregations naturally. Both species were originally housed in an 8 cm^2 area for 14 days and their space use in an enlarged

arena of 154 cm^2 was evaluated and compared against control groups of both species. Woodlice restricted their movements within the size of their original housing, with previously restricted males restricting the area used and previously restricted females restricting the distances travelled. While male cockroaches travelled shorter distances than females, the cockroaches did not spatially restrict their movements in the enlarged arena, indicating that they may be displaying a rebound effect.

My study demonstrated that previous experience in restricted housing does have an effect on subsequent space use in an enlarged area. This notion of previous experiences influencing later experiences is the foundation of learned helplessness. Learned helplessness is the passive response to mostly aversive stimuli in which an organism has no control over the outcome of the situation and thus gives up after repeated failure. Learned helplessness appears to be a plausible explanation for the space restriction in chimpanzees, striped mice and woodlice, as these three species restricted their space use based on the previous experience of less available space. Chimpanzees and striped mice had higher occurrences of restricted movements compared to woodlice, indicating that learned helplessness with respect of space use maybe graded according to neuronal complexity. I conclude that providing additional space may not address the welfare concerns of captive animals, because more space did not disrupt earlier spatial restriction. However, the implications of exposure to restricted space needs to be considered for all species in captive environments, especially animals in release programs, as exposure to restricted space may contribute to the expression of learned helplessness, with space use in an enlarged area being influenced by previous restrictions.

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Chapter 1

Rationale

Restricted space apparently causes stress for animals in captivity, with spatial restrictions contributing to memory and learning impairment. Therefore, providing appropriate housing for captive animals is an important concern for animal managers as it affects the well-being and breeding success of an animal (Morgan and Tromborg, 2007).

My study is concerned with understanding how captive animals, housed originally in restricted space, used additional space made available to them later. In particular, my project aimed to investigate whether animal space use was related to the neuronal complexity of a species.

One method of assessing the influence of neuronal complexity on space use, following spatial restrictions, is to consider species with varying neuronal complexity. To this end, my study considered 4 species with different neuronal complexity. This change of available space could have implications of how each species utilised the space in the enlarged area, by either keeping movements or in the case of the chimpanzees, inter-individual distances, restricted to the old housing size; by having no change in space use; or by having an increase in subsequent space use. Memory & learning, space use and navigation have been considered as they each contribute to gaining a holistic understanding of the space use of previously restricted individuals. The stress of a captive environment can influence learning and memory; this in turn can influence an animal’s space use.

Memory and learning

Learning and memory are 2 aspects of cognition (Duncan and Petherick, 1991). Learning is a process by which new information is acquired (Squire, 1987), while memory can be considered as the process by which the learned knowledge is retained and recalled (Bailey *et al.*, 1996); memory is thus a consequence of learning (Squire, 1987). Learning and memory give rise to expectation or anticipation which can allow for animals to regulate effort put into tasks (Duncan and Petherick, 1991). Learning and memory enable animals to track changes in the spatial and temporal distribution of food (Krebs and Inman, 1992), modify behaviour based on experience (Kandel, 2001), or relocate nesting sites for brood care, protection and shelter (Menzel and Müller, 1996). All animals have some capacity to learn, with the modification of their behaviour as a result of experience (Evans, 1984).

There are various types and forms of memory, such as long-term, visual and working memory, and each necessitates specific anatomical structures depending on the specific memory task (Goldman-Rakic, 1996). There are 2 main types of memory: explicit (or declarative) and implicit (or non-declarative) memory. Explicit memory is the conscious recall of information, such as places or faces, and is particularly well developed in the vertebrate brain (Bailey *et al.*, 1996). Implicit memory is the non-conscious recall of motor skills and includes simple associative forms (e.g. classical conditioning) and non-associative forms (e.g. habituation) (Bailey *et al.*, 1996). Understanding these types of memory is of importance to my study because of the differences in the way the test species used in my study retain information of being previously housed in restricted housing.

Spatial memory

Spatial memory is responsible for recording information about the surrounding environment and spatial orientation of an individual. The main structures and processes involved in spatial memory of mammals, insects and crustaceans are discussed below since representative of these taxa have been selected for study.

Mammals

The hippocampus plays an important role in terms of spatial memory processing (Becker *et al.*, 1980; Schenk and Morris, 1985). It is involved with spatial mapping and place learning which is distinct from other forms of learning such as cue or response learning (Nadel and Macdonald, 1980). The hippocampal system is differentially involved in tasks that require working memory, which is associated with flexible responses to a stimulus that changes from trial to trial, but is not involved with tasks that require reference memory, which is composed of fixed responses to a stimulus that remain constant from trial to trial (Olton and Papas, 1979).

Hormones and neurotransmitters mediate the spatial memory tasks. Acetylcholine is important for spatial navigation (Winkler *et al.*, 1995), corticosterone is important for spatial memory formation (Oitzl and de Kloet, 1992) and decision making processes (Sandi *et al.*, 1997), and epinephrine (adrenaline) is important for memory enhancement (Gold and van Buskirk, 1975). The amygdala, which plays a central role in the modulation and processing of emotions (von Gunten *et al.*, 2000), is critical for mediating the influence these hormones have in the hippocampus (McGaugh, 2000).

Insects

Arthropods generally have much smaller brains than vertebrates, but because they can also have smaller neurons, their brains can still be very complex (Loesel, 2005). Kandel and Abel (1995) found that the mammalian hippocampus and mushroom bodies of the *Drosophila* brain appear to share attributes of biochemical pathways of memory storage. The mushroom body of the insect is essential for short-term memory in odour discrimination tasks (de Belle and Heisenberg, 1994; Heisenberg, 1998; Zars, 2000), and is involved in place memory (Mizunami *et al.*, 1998).

Krashes *et al.* (2007) suggested that different lobes of mushroom bodies have different roles in memory, where neurotransmission of different subsets of mushroom body neurons contribute to memory acquisition, retrieval and stabilisation. Though mushroom bodies play a role in learning and memory, they are not the centre of memory formation; rather, they have an important role in a wider neural system that supports learning and memory (Mizunami *et al.*, 1998).

Crustaceans

Crustaceans and insects have many neural features in common (Strausfeld, 1998). Nonetheless, crustacean brains do not have mushroom bodies, and instead they possess accessory lobes and hemiellipsoid bodies. The accessory lobes are thought to be involved in higher order integration of visual, mechano-sensory, and olfactory information (Sandeman *et al.*, 1995).

Movement detector neurons (MDNs) from the lobula (third optic ganglion) appear to be the central elements for acquisition and retention of visual memory (Tomsic *et al.*, 2003). The study by Tomsic *et al.* (2003) on *Chasmagnathus,* found that the changes in the response of a group of MDNs closely reflected behavioural changes that come about during learning, and that the persistence of these changes corresponds with memory retention.

Stress effects on learning and memory

Stress can impede memory (Williams *et al.*, 1998) and affect spatial learning (Brucato *et al.*, 1996). Chronic stress impairs the rate of spatial learning in Sprague-Dawley rats, *Rattus norvegicus*,(Park *et al.*, 2001), has been shown to affect memory processes in tree shrews, *Tupaia glis*, (Ohl and Fuchs, 1999), and Wistar–Imamichi rats, *Rattus norvegicus,* showed impairment in maze learning performance after chronic stress exposure (Nishimura *et* *al.*, 1999). The impaired learning and memory from chronic stress is thought to be as a result of altered properties of hippocampal plasticity (Kim *et al.*, 2006). Since stress can have an effect on learning and memory in animals, for the purposes of my study, it is important to consider how animals will react to captive environments, which can be stressful, and how exposure to these stressful captive environments may impair learning and memory and thus influence space use of animals.

Space use

Some animals thrive in captivity while others suffer. These differences in success are dependent on constraints imposed on natural behaviours e.g. Clubb and Mason (2003), who looked at the pacing in carnivores, and stating that wide-ranging lifestyles in the wild predict the extent of infant mortality and stereotypy. Preventing the natural behaviours of an animal could lead to stress and frustration as well impairment on brain development, particularly in naturally wide-ranging species (Clubb and Mason, 2003). Although animals that have large home ranges in nature may require a large amount of space in captivity, it may not necessarily hold true for every situation. The space use of animals in nature is often determined by a variety of factors, such as feeding behaviour, with home ranges dependent on food availability, searching strategies (Price, 1999) or availability of possible mates (Cooper and Randall, 2007). For example, the ranging patterns of gorillas, *Gorilla gorilla beringei*, depend on food availability and quality, with the latter being deemed more important (Vedder, 1984). Therefore, the home range size of gorillas will be dependent on food availability; greater food availability could decrease home range size. However, home range size is sometimes unrelated to foraging. An animal may be motivated to explore an area for its own sake (Price, 1999; Leone *et al*., 2010) and would thus require a large amount of space in captivity regardless of food, as was seen in laboratory mice, *Mus musculus*, which explored new areas regardless of the composition of the enclosure (Sherwin and Nicol, 1997).

Among the many stressors that captive environments induce in animals, space limitation is one of the primary contributors of captivity-induced stress (Morgan and Tromborg, 2007). Space restrictions can have adverse effects on the behaviour of an animal (Arakawa, 2005), which is further exacerbated by a lack of enrichment (Newberry, 1995; Beattie *et al.*, 1996). Rats, *Rattus norvegicus*, reared in poor, restricted environments display a decrease in activity levels in open-field tests (Arakawa, 2005), and pen size affects the growth rate and levels of aggression of pigs, *Susscrofa domesticus*, (Morgan and Tromborg, 2007).

The perception that an animal has about space influences how available space is used (Sherwin and Nicol, 1997). Animals develop an expectation about their environment through learning or instinct and when an animal is faced with a challenge, the response employed will depend on this expectation and the situation itself (Meehan and Mench, 2007). If there is a mismatch between an animal's expectation and the prevailing environment, frustration develops. If the problem is controllable (e.g. needing to open a latch to gain food that was previously inaccessible) frustration decreases, but if not solved (e.g. not being able to access the food at all) frustration will increase, leading to stress because of physiological and behavioural changes (Meehan and Mench, 2007).

Determinants of space use in captivity

For many species, the quality of space appears to be more important than the quantity of space (Stoinski *et al.*, 2001; Hosey, 2005). In nature one of the most common factors affecting space use is the tendency to confine activities to particular areas in the home range (Horne *et al.*, 2008). Animals generally use space disproportionately based on ecological factors, where some areas are used more than others (Samuel *et al.*, 1985; Marriott and Meyers, 2005), which will depend on the availability of resources (Matthiopoulos, 2003). In the natural environment, animals will move to areas where required resources, such as food or shelter are available; the same would happen in captive environments. In natural habitats, animals orient themselves in specific ways depending on available objects, like perches and vegetation cover to scan for predators. In captivity, objects available are often used in a similar manner based on innate survival tendencies, e.g. trees may be used to scan the enclosure or may be used by animals to hide from perceived threats, such as large crowds of people (Marriott and Meyers, 2005).

The presence of barriers can also have an impact on how space is used. Gorillas (Stoinski *et al.*, 2001; Ross *et al.*, 2009) and chimpanzees, *Pan troglodytes*, (Ross *et al.*, 2009) show a strong preference for being near structures such as walls, mesh barriers and corners. House mice, *Mus domesticus*, tend to remain close to walls or other objects, allowing them to be in contact (i.e. thigmotaxis) with the environment and aiding in protection (Jensen *et al.*, 2003). Though not the only sensory cue of importance, tactile information plays an important role in environment familiarisation (Basil and Sandeman, 2000) and is also important for invertebrates like cockroaches, *Periplaneta americana,* (Camhi and Johnson, 1999) crayfish, *Orconectes rusticus,* (Alberstadt *et al.*, 1995) and woodlice, *Porcellio scaber,* (Hughes, 1987), where tactile cues can aid in guiding locomotion and influence the direction in which they turn. In addition to tactile cues, landmark identification can also aid in guiding locomotion, helping animals to orientate themselves in space (Collett *et al.*, 1986).

Navigation

Many species use landmark identification to locate target areas (Hoffmann, 1983; Vannini and Cannicci, 1995; Collett, 1996) and the orientation of many species is based on memorising space. Locations are either memorized by an egocentric coding, based on route-based information, or an exocentric coding, which is based on location-based information (Benhamou *et al.*, 1990). Navigation strategies that are employed to locate these target areas can differ depending on the species and the purpose of movement, such as locating food (Durier and Rivault, 2000) or locating areas for shelter (Kingsford *et al.*, 2002).

Place memory in mammals has usually been considered in terms of cognitive maps as proposed by Tolman (1948), where an animal’s world is centrally represented in the brain and being constantly updated (Mizunami *et al.*, 1998). In insects, such as bees and ants, place memory involves image matching where an insect moves until its current retinal image matches a previously stored view of the environment. Image matching depends on the memory of patterns of defined size and shape (Collett, 1996). While navigation for insects involves memory it is not solely dependent on place memory; insects often maintain a constant angle with the direction of sunlight or even with a plane of polarisation. These basic mechanisms of orientation may involve learning (Evans, 1984).

Sex and age effects of space use

Space use can differ between the sexes. In meadow voles, *Microtus pennsylvanicus*, the daily ranges of males are greater than the ranges of females (Madison, 1980). Male chimpanzees tend to band together and defend large ranges whereas females are more exploratory, leaving their home ranges at sexual maturity and at times associating with more than one chimpanzee community (Williams *et al.*, 2002).

Age also has an effect on space use. The space use of broiler chickens, *Gallus gallus domesticus*, declines with increasing age (Newberry and Hall, 1990). In rats, *Rattus* *norvegicus*, the juveniles are sensitive to limiting space (whereas older rats are sensitive to stocking density) but the adverse effects that space limits had on individuals weakened with maturity (Arakawa, 2005).

Newberry (1995) points out that previous experience is also an important consideration with regard to space use, and the movements of an animal in, for example, a new area may depend on the early or previous experiences of that animal. An interesting case study is provided in white leghorn chickens, *Gallus gallus domesticus,* that were brooded for 7 weeks in separated pens and were then allowed to roam around all pens. When given the option to roam, they did not freely intermingle and preferred remaining in the vicinity of the pen where they were brooded (Newberry and Hall, 1990). A possible explanation for this limitation on space use is that the chickens were afraid (i.e. neophobic) of the novel environment (Jones, 2002) and thus preferred staying in the familiar brooding area. Alternatively, this example of the white leghorn chickens can be explained by the learned helplessness hypothesis, where animals perceive that a situation is independent of their behaviour and thus they inhibit their responses based on the expectancy that their actions yield no alternative outcome (Martinko and Gardner, 1982). So with regard to the white leghorn chickens, the chickens were not moving beyond the environment they had been exposed to originally even though there was an increase in the amount of available space. The chickens may have had the perception that they would not able to move beyond the point of the original barrier that had previously separated the pens from each other.

Objectives and aims

The study has 2 objectives

- To establish whether the previous experience of an individual or of a group of individuals in a restricted space influences the subsequent use of space in larger areas.
- To establish whether the space use in the enlarged area is related to the neuronal complexity of the test species.

Four species were selected for study, including chimpanzees, *Pan troglodytes,* striped mice, *Rhabdomys dilectus dilectus,* German cockroaches, *Blattella germanica,* and common woodlice, *Porcellio scaber.*

Aim 1. The main aim is to ascertain space use of 4 species by quantifying the surface area used by each species.

- Question: If previous experience in restricted space does influence subsequent space use, I ask whether there is a relationship between space use and neuronal complexity.

Layout of the dissertation

Because of the phylogenetic differences among the species and the idiosyncrasies of the housing, sociality, and potential experimental manipulation of the species, I have provided specific aims and predictions for each species separately in the following chapters. The sampling duration per species was scaled according to the relative body size, movement patterns and activity levels of each species.

Apart from the present chapter (General Introduction), my dissertation comprises of 4 experimental chapters (Chapters 2-5) and a general discussion chapter (Chapter 6). Chapter 2 focuses on the space use of the chimpanzees, *Pan troglodytes*. The age, sex and behavioural effects as well as the influence of shade on space use are considered. Chapter 3 focuses on the space use of striped mice, *Rhabdomys dilectus dilectus,* where test subjects could be assigned to treatment and control groups to assess whether space use is influenced by previous experience. Additionally, the sex and personality effects of striped mice on space use are considered. Chapter 4 considers the space use of woodlice, *Porcelio scaber*, where treatment and control groups were created to assess whether previous restrictions influence subsequent space use of male and female woodlice. Chapter 5 considers the space use of male and female cockroaches, *Blatella germanica,* and compares the space use of individuals from control and restricted groups. Chapter 6 is a general discussion and conclusion section. One reference section is provided. Because of the abovementioned format, there may be some repetition of methodological details or discussion. Figures and tables are numbered in sequence for the entire dissertation, and not per chapter.

Chapter 2

Experiment 1: Chimpanzees

Introduction

Chimpanzee biology

Chimpanzees, *Pan troglodytes,* live in social groups of 20 to over 100 members of both sexes (Goodall, 1986). Chimpanzees are semi-territorial omnivores (Busse, 1978) and have a fission-fusion society (Williams *et al.*, 2002), where males and females have different space use patterns. Males are philopatric and defend a territory, whereas females move away from their natal group; females shift their core areas and join and leave male territorial groups at any time (Williams *et al.*, 2002; Reynolds, 2005). Female space use can be related to male-defended ranges and female composition. Females may alter their space use patterns to stay within male-defended boundaries or their patterns may be influenced by feeding competition with other females (Williams *et al.*, 2002). Females generally spend time on their own, i.e. with no other adults present, rather than forming cohesive groups (Wrangham and Smuts, 1980), and their ranges may overlap over 2 groups (Williams *et al.*, 2002). Food resources are an important determinant of space use in nature, influencing the positions of home ranges of males and females (Lwanga, 2006).

Social learning is important for the acquisition of novel behaviour (Boesch, 1991). Chimpanzees have a good memory and a high capacity for learning and solving problems, acquiring knowledge through trial and error, observational and perceptual learning, where positive and negative reinforcement aid in the learning process (Goodall, 1986). Young chimpanzees learn about their environment through play and exploration, and these early experiences can have a subsequent effect on adult learning skills (Goodall, 1986).

Free-living chimpanzees live mainly in forests where they experience relatively stable temperatures seasonally and they experience nearly constant shade provided by the tree canopy cover (Goodall, 1986), indicating that shade is important to chimpanzees. Temperature and sun exposure both influence chimpanzee activity, behaviour and space use; where chimpanzees would increase their time on the ground and resting, and decrease their feeding, with increasing temperatures. Time exposure to sunny areas was temperature dependent with chimpanzees moving to dense, cool areas during the hottest times of the day (Kosheleff and Anderson, 2009). In captive environments, chimpanzees prefer spaces as high as 15m above the ground and areas with features such as columns, edges and corners which are used for buffering against environmental extremes (Ross and Lukas, 2006).

Inter-individual distance between chimpanzees in nature is not well recorded in the literature, especially since free-living chimpanzees do not form spatially cohesive social groups, with individuals associating with different subgroups, so that the subgroups constantly change composition and size (Chapman *et al.*, 1995). These fission-fusion societies, as well as the dense forest habitat of the chimpanzees, are confounding factors for evaluating the distances between individuals and to establish whether they are part of the same subgroup. Consequently, subgroups are generally categorised by the number of individuals in the group rather than by the amount of space occupied (Nishida, 1968; Chapman *et al.*, 1995; Matsumoto-Oda *et al.*, 1998). Nonetheless, some studies on free-living chimpanzees considered subgroups to be individuals with inter-individual distances between 35 m (Bates and Byrne, 2009) and 100 m (Wrangham and Smuts, 1980) during activity.

Aims and predictions

In addition to the main aim - to ascertain space use of 4 species by quantifying the surface area used by each study species (Chapter 1) - I had 4 additional aims for the study of space use by the chimpanzees, each with its own prediction/s.

In the following text ‘space restricted’ or ‘restricted subgroup space use’ refers to the dimensions that a subgroup occupies at any one point in time i.e. covering the dimensions of the old enclosure. Therefore if one subgroup is more restricted than another, that subgroup is staying within the dimensions of the old enclosure more often than the less restricted subgroup.

Aim 2. Examine the space use of males and females to assess whether space use is sex specific.

- I predict that females will be less space-restricted than males, as female chimpanzees naturally move around more than males, as is seen in nature (Williams *et al.*, 2002).

Aim 3. Establish space use by adults and juveniles to assess whether space use is age specific.

- Assuming there are differences in space use with regard to age, I predict juveniles to be less space restricted than adults because juveniles of most primate species tend to be more active than adults, as has been observed in captive chimpanzees and bonobos, *Pan paniscus*, where play is at its highest in juveniles (Palagi *et al.*, 2004). Some of the youngest juvenile chimpanzees at the Johannesburg Zoo also spent the least amount of time in the old enclosure and the youngest chimpanzee was born in the new enclosure. Therefore, juveniles may use space differently to adults in the enlarged enclosure as they have had less exposure to restricted housing.

Aim 4. Ascertain the association between space use and behaviour by determining the predominant behaviours displayed by individuals when they were part of a subgroup and not part of a subgroup.

- I predict that small subgroups would be characterised by higher frequencies of space restricting behaviours (e.g. inactive behaviour, socio-positive behaviour) while large subgroups or individuals not part of any subgroups, would show higher frequencies of walking or behaviours like locomotory play.

Aim 5. Establish the association between space use and shade provided by trees or walls to assess whether space use in chimpanzees is influenced by the presence of shade.

- I predict that individuals will restrict their movements and activities to areas where there is shade, since chimpanzees are naturally found in areas where there is high tree canopy cover (Goodall, 1986). If so, spatial restriction might be influenced by the available shade.

Study subjects

During my study, the group of chimpanzees at the Johannesburg Zoo comprised 4 males and 4 females. The 4 males consisted of 2 adults (Yoda and Thabu), 1 adolescent (Amber) and 1 weaned juvenile (Charles). The females consisted of 3 adults (Lilly, Daisy and Zoe) and 1 weaned juvenile (Joyce). Yoda (the dominant male), Amber, Charles, Zoe and Joyce were the offspring of Thabu and Daisy. Lilly (the dominant female) was acquired from an Angolan zoo by the Jane Goodall Institute. All individuals, apart from Charles, were originally housed in a smaller enclosure of 100 m^2 (before 2004), until they were moved to a new enclosure of 2500 m^2 (after 2004).

The chimpanzees were fed fruits, vegetables, primate pellets and primrose oil twice daily at 09:30 and at 15:30. Their food was scattered randomly around the enclosure, thus preventing clustering at any 1 point in the enclosure, and to stimulate foraging activity.

Old enclosure

Until 2004, the chimpanzees were part of either an orphan group or a family group. Each group was housed in separate 10 m x 10 m enclosures, each surrounded by a water moat on 2 sides and walls on the other 2 sides (Figure 1). The enclosure of the orphan group had 2 public viewing points in front of the water moat.

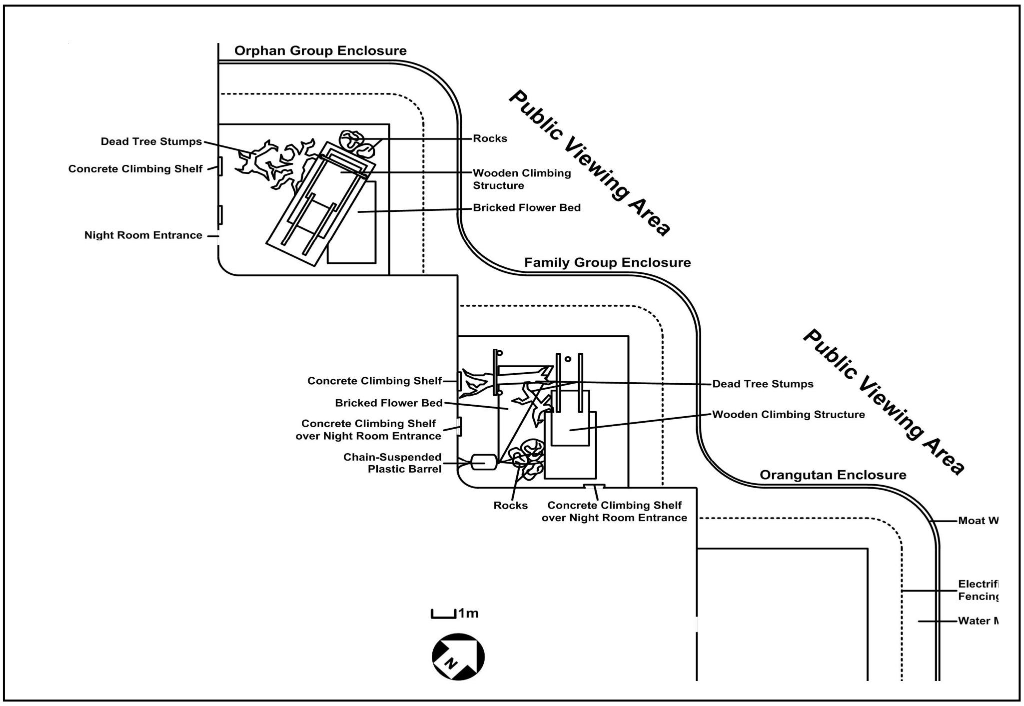


Figure 1. The old chimpanzee outdoor enclosures at the Johannesburg Zoo (prior to 2004; Courtesy of L. Duncan).

Within both enclosures, there were rocks, ropes, climbing shelves and dead tree stumps for climbing. There were also night rooms for each group with jungle gyms and ropes (Figure 1).

New enclosure

During my study (2009), the chimpanzees were housed together in a large enclosure of 2500 m^2 (Figure 2). Only the original family group (Daisy, Thabu, Amber, Joyce, Charles, Zoe and Yoda) was still present and 1 orphan individual, Lilly, who was housed with the family group. The group had access to an indoor enclosure at night (which had jungle gyms and ropes). My study was done on the space use of the chimpanzees in the outdoor enclosure, which was divided into 2 sections by a large wall with a connecting door. There were water access points, ropes, trees, tree stumps and plastic barrels for swinging and climbing in both sections. The walls of the enclosure were approximately 8m high. Electric fencing was present along the top of the walls and along the water access points. There were 3 different public viewing points: 3 large, ground level windows in the left wall; an open viewing area close to the water access points; and a 2.5 m platform which had a view of both sides of the enclosure.

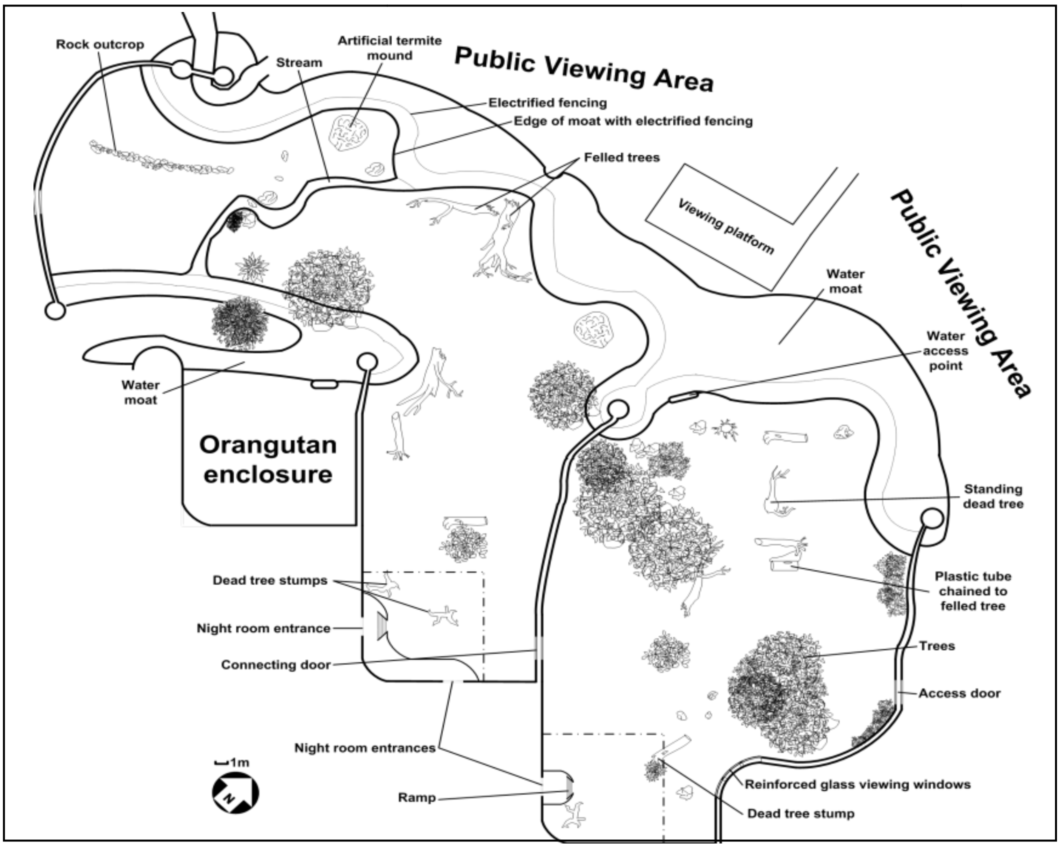


Figure 2. The new chimpanzee outdoor enclosure at the Johannesburg Zoo (after 2004). Dashed lines in the bottom left represent the size and location of the original housing areas for the orphan and family groups (Courtesy of L. Duncan).

Sampling

Space use and behaviour of the chimpanzees were both sampled. I sampled space use by evaluating subgroup and individual movements over space and time. In addition to behavioural sampling, I recorded the season, weather and use of shaded areas. Details are provided below.

Space-use

Space use sampling was done for 60 non-consecutive days (i.e. sampling sessions) between March and July 2009. Each observation lasted 1 hour and was conducted in the morning, mid-morning or afternoon on different days. Sampling took place after the chimpanzees had been fed. During feeding, which was at 9:30am, food was scattered around the enclosure to encourage the chimpanzees to search for food. This scatter feeding by the zoo keepers, as well as my sampling approximately half an hour after they had been fed, reduced space-use bias because the chimpanzees did not congregate in a specific place each day to feed and thus reduced the potential bias in the data sampling.

Space use by the chimpanzees was recorded by taking photographs with a Kodak C613 camera set at 3X optical zoom. To enable both the photography and behavioural observations, I used a simultaneous sampling technique. Samples were taken every 5 minutes in which photographs were taken and behaviours of individuals were recorded simultaneously. Sampling sessions were 1 hour long, resulting in 12 data points each of photographs and observations per sampling session.

Photographs were taken of the chimpanzee subgroups. A subgroup was considered as comprising of 2 or more individuals as well as any individual that was less than 10m away from another individual. This distance was used to compare space use against the previous housing of 10m x 10m. I also recorded excursions by individuals, which was defined as an individual moving away from and returning to the subgroup in under 5 minutes; any absence over 5 minutes was not considered as an excursion. If at any given sampling time, all the chimpanzees were scattered around the enclosure (all individuals >10 m apart) and did not form any subgroups, they were recorded as scattered and no photographs were taken.

At the end of the sampling sessions, I used the photographs to identify and assess the size of the areas occupied by each chimpanzee subgroup at an instantaneous time sampling interval of 5 minutes (Figure 3).

Subgroup within 10 m x 10 m ***Subgroup >10 m x 10 m*** ***No subgroup formation***

Figure 3. Examples of chimpanzee subgroups of different sizes and the absence of subgroup

In order to improve sampling accuracy, 2 methods were used to measure the area used by subgroups at 1 time sampling point. In the first method, the positions of the chimpanzees that formed a subgroup were plotted onto a map of the enclosure drawn to scale. The area occupied by that subgroup, every 5 minutes for 1 hour, was evaluated using a grid that ranged from 10m x 10m to 20 m x 20 m. An edge effect of 1 m was included in the grid measurement, resulting in grids of 11 m x 11 m to 21 m x 21 m (Figure 4). The area that the chimpanzees occupied in the outdoor enclosure was matched against 2 categories: within the 11m x 11m grid or greater than the 11m x 11m grid. Only 2 categories were evaluated to assess whether or not space use was influenced by the size of the previous housing.

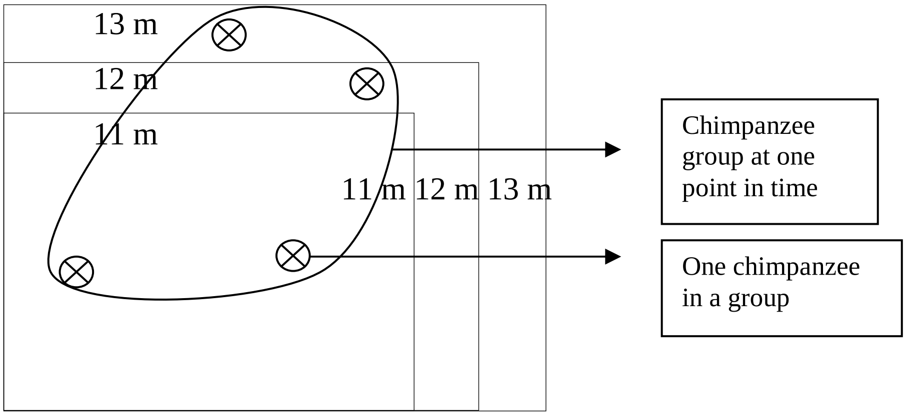


Figure 4. Representation of the grids that were use to assess space use of chimpanzee subgroups.

In the second method, measurements were taken in the enclosure from selected landmarks (e.g. from a tree to a rock or a tree to a wall) to obtain reference distances within the enclosure, and to ground-truth the observations. The measurements were taken when the chimpanzees were in their night room. These distances were used to estimate the distances between individuals within a subgroup. The locations of individual chimpanzees were plotted on a map of the enclosure using these estimated distances and the area covered by the subgroups was evaluated using the grid method (Figure 4). The measurements were added together and averaged to gain the total of measurements that fell within, and outside of 11 m x 11 m. The data collected from both sampling techniques were used to ascertain whether chimpanzees restricted their movements to the space covered by the old enclosure size, or whether their space use was greater than that of the old enclosure.

Space use was evaluated in 2-dimensions only, and any individuals in trees were considered to be within a subgroup (e.g. 11 m x 11 m). When evaluating the area of space used, barriers between individuals were considered, so that if there was a rise or a wall blocking 1 chimpanzee from the view of another, they were not considered to be part of the same subgroup, as suggested by Bettinger *et al.* (2005), who maintained that visual separation was an important mechanism for decreasing aggression, as individual chimpanzees did not perceive one another when obstructed by physical barriers.

Subgroup and individual movements over space and time

The spatial and temporal movements made by subgroups were also evaluated. To evaluate space-use temporally, I recorded how the subgroups moved within an hour session, i.e. whether the subgroup remained within an 11 m x 11 m area, increased their space use to a larger area, or if no subgroups formed. This was done for all 60 hours sampled.

To evaluate space-use spatially, I recorded whether and how chimpanzee subgroups within 11 m x 11 m moved around the enclosure, i.e. did they stay in the same area or move to a different area within the enclosure; this was done only for subgroups within 11 m x 11 m since this was the focus of my study. Only 44 of the 60 sessions met this criterion and were used for further analyses. Individual movements were also recorded to ascertain which individuals moved within and between subgroups. A matrix was created to record how often each individual was part of a subgroup and was also used to assess how often other individuals were part of the same subgroup, e.g. Thabu was in the same subgroup as Daisy x-number of times. This was done to establish which individuals interacted with each other the most number of times. Understanding how individuals formed subgroups was of importance because it is indicative of group composition, which is a component of how an individual used the available space and could help identify whether adult males, adult females or juveniles were more readily forming subgroups.

Behaviour sampling and recording use of shaded areas, weather and season

During the sampling sessions, the behaviour of each chimpanzee was recorded every 5 minutes, resulting in a focal individual time sampling protocol, with an instantaneous recording rule. The simultaneous sampling technique discussed in ‘Space-use sampling’ was used. The behaviours were sampled according to 9 behavioural categories (Table 1).

The use of sunny or shaded areas by the chimpanzees was recorded during each behaviour recording. Individual chimpanzees were recorded as being in the sun only if they were completely in the sun. These data were used to investigate whether or not chimpanzees used particular parts of their enclosure because of the presence of shade.

Table 1. Behaviours that were scored for chimpanzees at the Johannesburg Zoo.

Behaviour	**Definition**
Abnormal	Behaviours included chronic masturbation, unusual repetitive behaviour, self biting or hair pulling
Climbing	Climbing trees, swinging on ropes
Excursions	The moving away and returning of individuals from a subgroup in under 5 minutes
Foraging	Eating food that had been scattered around the enclosure and drinking from water moat
Inactive	Resting or sleeping
Interacting with public	Individuals approaching the windows or fences and engaging with the public, including chimpanzees knocking on windows or clapping hands
Play	Any type of play: social play with other chimps – wrestling, rolling, chasing each other; playing alone by swinging from ropes or playing with objects like sticks
Socio-negative	Agonistic behaviour directed towards other chimpanzees, including screaming, chasing and fighting with other chimpanzees
Socio-positive	Affiliative behaviour, such as grooming, embracing directed towards or received by other chimpanzees

The weather was recorded in order to compare the space use of the chimpanzees under varying environmental conditions. The weather type was scored according to the following categories: sunny, sunny with clouds, and overcast.

Season was categorised based on the time of the year the sampling took place and was classified broadly as late summer/autumn (sampling before 1st June 2009) and winter (sampling after 1st June 2009).

Data analysis

Space use data were analysed using a chi-squared analysis to evaluate whether there were differences between the number of small subgroups (11 m x 11 m) to large subgroups (>11 m x 11 m) that formed during the entire sampling period, for summer and winter and under different weather conditions. The chi-squared analyses were run using InStat version 3 (GraphPad Software, 2003). Since there were only 5 overcast days, comparisons were made between these 5 days and randomly selecting 5 days under each of the sunny and cloudy weather categories; this was done 3 times by selecting 3 x 5 days from the sunny and cloudy categories. A heterogeneity chi-squared analysis was used to compare weather influences on space use; a heterogeneity chi-squared test is appropriate when analysing multiple subgroups of a larger data, since it compares each group (3 in my case) separately against the average of the overall data set (Zar, 1996).

Space use and chimpanzee presence in the shade/sun was evaluated for an individual chimpanzee and not a subgroup basis because some individuals forming a subgroup could have been in the sun while others could have been in the shade, so that a subgroup of chimpanzees could have been occupying space in the sun as well shade at 1 sampling point. These data were then analysed based on whether the individual in the sun/shade was part of a subgroup that was covering an area equal to or less than 11 m x 11 m, greater than 11 m x 11 m or was not part of any subgroup. The data were analysed using a Generalised Linear Model (GLZ) as this allowed for comparisons for occupancy in sunny and shaded areas between all 3 subgroup size categories, making no assumptions of normality or homogeneity of variance and permitting the data to be fitted to a binomial distribution. I further investigated the consistency of space use and whether chimpanzee space use was constant over space and time. I used a transition matrix to evaluate whether the chimpanzee subgroups were consistent in their space use over time, as described below.

Each space-use size category was assigned a number: 11 m x 11 m = 1; >11 m x 11 m = 2; and no subgroup formation = 0. No subgroup formation meant that all chimpanzees were greater than 11m from each other; thus they were not forming what was considered a subgroup (individuals less than 11m apart) for this experiment. For each 1 hour observation session, a number score (0, 1, 2) was assigned for space use at every 5 minute sampling interval, resulting in a 12 number sequence for each hour. I then recorded how many changes or consistencies there were per space-use size category.

An example of a 1 hour sample: 1 1 1 2 2 1 2 0 1 1 1 1. Staying within a 1 category occurred 5 times; transition from 1 to 2 occurred twice, transition from 0 to 1 occurred once, etc. Transitions were then recorded in a matrix and the proportion of transitions was evaluated for the whole sampling period (Table 2).

Table 2. An example of the table used for chimpanzee group transitions.

Transition **From**	 **To**	**Proportion**
0	**0**	0
1	**1**	5/11 = 0.45
2	**2**	1/11 = 0.10
Transition to a different space-use category **E.g. 1 to 2, 2 to 0, etc...**		5/11 = 0.45

The transitions over space were used to evaluate how chimpanzee subgroups within 11 m x 11 m moved over the enclosure. The change over space was evaluated by establishing how often a subgroup remained in the same place and how often a subgroup moved to a different area, which was evaluated by any group movement 11m from the original group position. A chi-squared analysis was used to analyse the differences between moving around the enclosure and remaining in the same place.

For the behavioural data, abnormal behaviour occurred rarely (<2 % of all observations) and was not considered for further analysis. A Factor Analysis was performed on the behavioural data to examine which behaviours rarely occurred. The first 2 factors of the Factor Analysis were considered and they cumulatively explained 35% of the dataset. Socio-negative (first: second factor - 0.012; 0.22), Excursions (0.26; -0.144) and Interaction with the public (0.26; -0.04) had the lowest factor loadings and were excluded from further analysis.

The behavioural data and shade/sun exposure data were analysed using a GLZ with a binomial distribution and probit link function, in which I tested whether there were differences in the behaviours (response category) between age and sex (adult male, adult female and juvenile) and grouping categories (subgroups that were smaller than 11 m x 11 m, larger than 11 m x 11 m, and when individuals were not part of any subgroups).

An all effects model from the GLZ was used to ascertain which variables had a significant effect on the model output. Based on these results, appropriate first, second and/or third order effects were selected using user-defined protocols in the final model selection. Beta coefficients and confidence intervals (95%) were used to detect specific differences in the categorical variables when the Wald statistics for the effects were significant. GLZ analyses were run in Statistica version 6 (StatSoft, Inc. 2001).

An analysis was conducted on the interactions of individuals compared to the likelihood of interaction with each member of the chimpanzee group. For this, a matrix of how often individuals were part of the same subgroup was analysed using the software Matman™ (De Vries *et al.*, 1993). The matrix was used to calculate adjusted residuals with positive (occurring more often than expected by chance) and negative (occurring less often than expected by chance) residuals calculated and expressed according to a Z-distribution.

In the following text subgroup sizes will be labelled “small” for subgroups within 11m x 11m and “large” for subgroups larger than 11 m x 11 m.

Experimental procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (clearance number 2007/57/01).

Results

Space use

Total space use

The space use of chimpanzees was evaluated by examining the frequency of chimpanzees being in small subgroups and large subgroups. Space use was evaluated for the 60 hour sampling sessions, regardless of seasonal and environmental effects. Chimpanzees formed small subgroups significantly more frequently (97%) than large subgroups (3%) ($\chi^2_1 = 702.39$, $p < 0.001$).

Seasonal variation

The space use of subgroups was then categorised according to season. There was no significant difference between summer and winter ($\chi^2_1 = 1.54$, $p = 0.215$). In winter, small and large subgroups formed 98% and 2% of the time respectively and in summer small and large subgroups formed 97% and 3% of the time respectively.

Weather

Subgroups were also categorised according to their occurrence during different weather types, namely sunny, cloudy and overcast. There were no significant differences in space use with respect to the 3 weather categories ($\chi^2_2 = 0.84$; $p = 0.900$; heterogeneity χ^2), with the chimpanzees occurring in small subgroups (97%) more often than occurring in large subgroups (3%) on sunny, cloudy and overcast days

Age and sex

There were differences in space use of adult males, adult females and juveniles. Following the all effects model protocol, age/sex, subgroup size and subgroup size*age/sex were significant predictors of the space use in the final GLZ model (Table 3).

Table 3. Results from the GLZ analysis analysing the space use of adult male, adult female and juvenile chimpanzees.

	Statistics results
Age/sex	Wald $\chi^2_2 = 122.96$, $p < 0.001$
Subgroup size	Wald $\chi^2_2 = 3521.52$, $p < 0.001$
Subgroup size*age/sex	Wald $\chi^2_4 = 94.77$, $p < 0.001$

Specific differences were identified using beta estimates and confidence intervals (95%). Whiskers on the graph represent 95% confidence limits as exact frequency values were plotted on the graph (Figure 5). For the subgroup size*age/sex interaction, adult males participated in small subgroups significantly less often than adult females and juveniles. There was a significant difference between adult female and juvenile presence in large subgroups, with adult females participating more than juveniles.

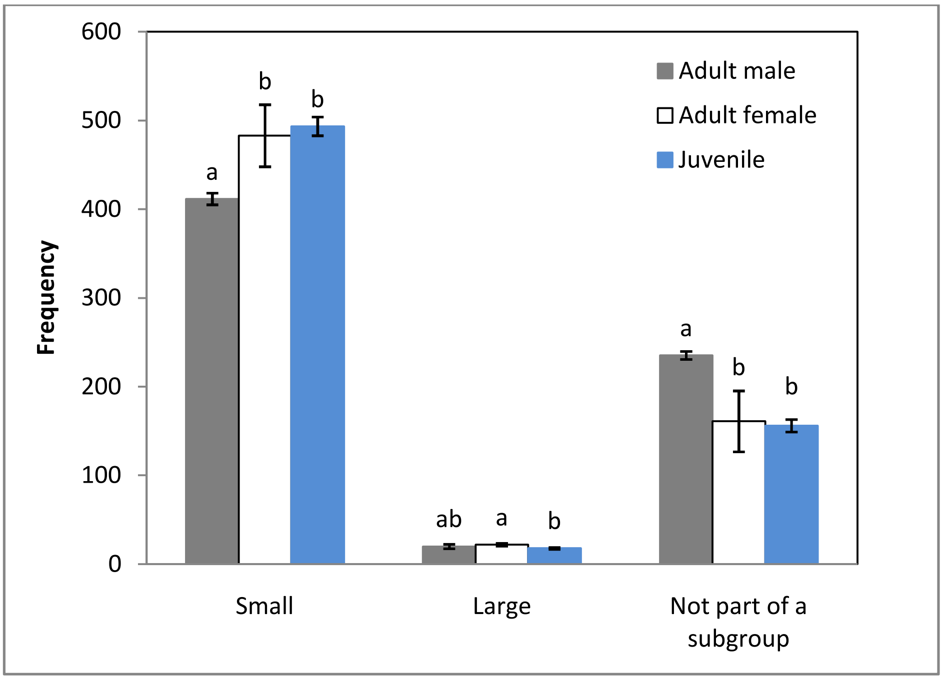


Figure 5. Mean frequency of presence in 3 subgroup categories for adult male, adult female and juvenile chimpanzees. Bars with the same letters within each subgroup size category (small, large, not part of a subgroup) are not significantly different. Whiskers denote 95% confidence limits.

Adult males were not part of a subgroup significantly more often than adult females and juveniles. Not considering the sex and age effects on subgroup formation, small subgroups formed more frequently than no subgroup, which occurred more frequently than large subgroups (Figure 5).

Transitions

Temporal

Chimpanzee sub-groups remained as small subgroups (0.920) more often than they did in large subgroups, not forming a sub-group or moving to a different space-use size category. The chimpanzee sub-groups consistently remained within the same space-use size category over the entire sampling period (Table 4).

Table 4. Proportion of transitions and consistencies between size classes of chimpanzee subgroups. (0 = no subgroup, 1 = small subgroup, 2 = large subgroup)

Transition From	**To**	**Proportion**
0	**0**	0.002
1	**1**	0.920
2	**2**	0.014
Different space-use category		0.065

Space

There was a significant difference between chimpanzee subgroups remaining in the same area compared to those moving to different areas within the enclosure (χ^2_2=256.46, $p<0.001$); subgroups remained within the same area 77% of time and moved to other areas 23% of time. The chimpanzee subgroups were therefore restricting their movements over space.

Behaviour and space use

The behaviours performed varied among individuals in different subgroup sizes over the total sampling period. Subgroup size, behaviour and subgroup size*behaviour were significant predictors of chimpanzee space use in the final GLZ model (Table 5).

Table 5. Results from the GLZ analysing the behaviour of adult male, adult female and juvenile chimpanzees while part of subgroup of different sizes.

	Statistics results
Subgroup size	Wald χ^2_2=7135.43, $p<0.001$
Behaviour	Wald χ^2_5=430.70, $p<0.001$
Subgroup size*behaviour	Wald χ^2_9=712.11, $p<0.001$

Collectively, small subgroups had a behavioural profile distinct from large subgroups and not being part of a group (Figure 6). For the behaviours, inactivity was the most common behaviour, followed by socio-positive, play and walking. Inactivity and socio-positive behaviour were displayed significantly more often than the other 4 behaviours. For the sub-group size*behaviour interaction, inactivity was significantly greater when chimpanzees were not part of any subgroups, compared to when chimpanzees were part of a subgroup. Socio-positive behaviour only occurred when chimpanzees were part of a subgroup but there was no difference in socio-positive behaviour between small or large subgroups (Figure 6). Walking occurred more frequently when individuals were not part of a subgroup, with no differences seen between large and small subgroups. The occurrence of playing, foraging and climbing behaviours was not different between the 3 subgroup types, with foraging and climbing being displayed the least of all the analysed behaviours.

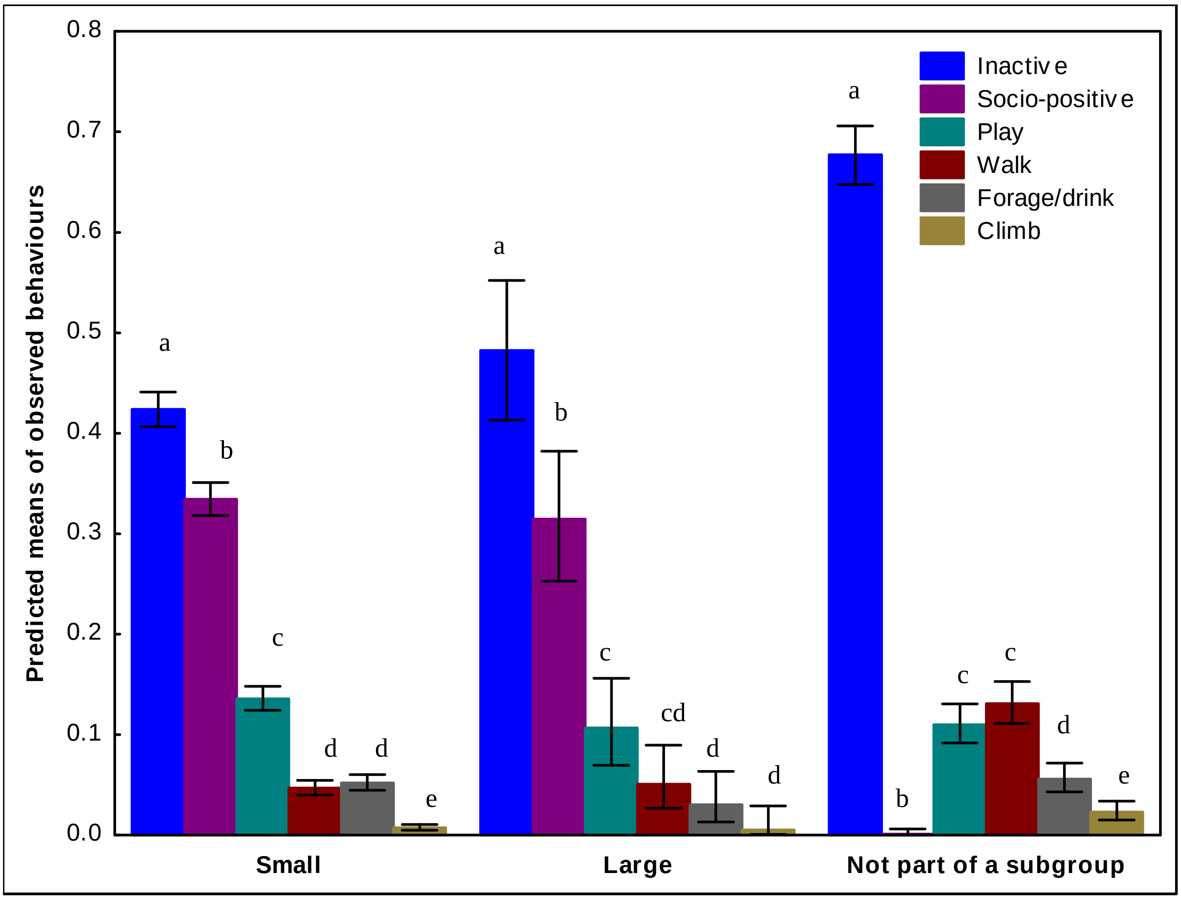


Figure 6. Predicted means of total observed behaviours performed by chimpanzee subgroups or by chimpanzees not part of a subgroup over the 60 day sampling period. Bars with the same letters within each subgroup size category (small, large, not part of a subgroup) are not significantly different. Whiskers denote standard error according to least squares means.

Sun/Shade and space use

Chimpanzee subgroups and individuals were categorised according to their occupation of sunny and shaded areas. Only their presence in sunny and shaded areas and subgroup size*sun/shade were significant predictors of chimpanzee space use in the final GLZ model (Table 6).

Table 6. Results from the GLZ analysing the presence of subgroups types in sunny and shaded areas. p-values highlighted in bold are significant.

	Statistics results
Presence in sunny and shaded areas	**Wald χ^2_1=366.78; p<0.001**
Group size	Wald χ^2_2=0.00; p=1.000
Subgroup size*sun/shade	**Wald χ^2_2=38.41; p<0.001**

Chimpanzees occupied shaded areas more often than sunny areas (Figure 7). For the subgroup size*sun/shade interaction, individuals were present in shaded areas more often when they were not part of a subgroup compared to being part of small subgroups; there was no difference between small and large subgroups (Figure 7). Group size did not have a significant effect in the final GLZ model (Table 6).

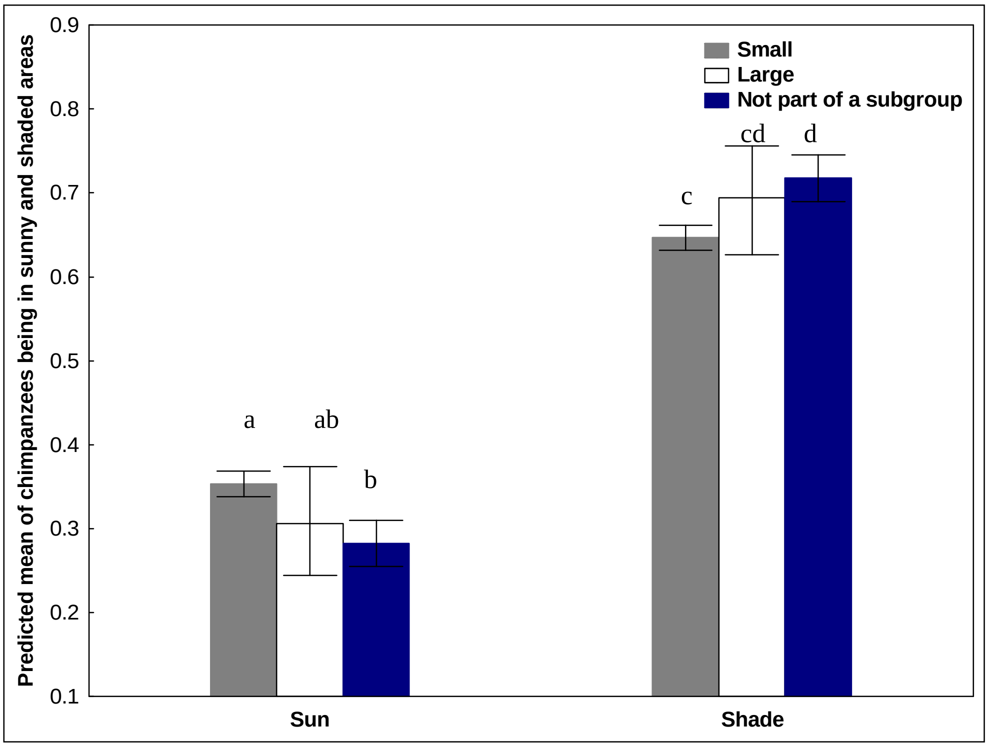


Figure 7. The presence of chimpanzee subgroups in sunny and shaded areas of the enclosure when they were part of small and large subgroups and when they did not form subgroups. Bars with the same letters are not significantly different. Whiskers denote standard error according to least squares means.

Behaviours and interactions of individuals

Descriptive statistics are presented for the dominant behaviours performed by individuals and individual interactions because the 8 individuals displayed different levels of each behaviour, precluding the use of probability statistics. For this reason, behaviours are summarised and presented as percentages of occurrence (Table 7). When being part of a subgroup, different individual chimpanzees displayed particular behaviours more frequently than others. The most predominant behaviour was inactivity followed by socio-positive behaviour and play.

Table 7. Percentage occurrence of the most and second most predominant behaviours performed by individuals when they were part of a subgroup.

	Individual	**Predominant Behaviour**	**%**	**2nd most predominant**	**%**
Adult Males	**Thabu**	Inactive	75	Socio-positive	16
	Yoda	Inactive	49	Socio-positive	38
	Amber	Inactive	55	Socio-positive	21
Adult Females	**Lilly**	Inactive	62	Socio-positive	23
	Zoe	Inactive	63	Socio-positive	28
	Daisy	Socio-positive	50	Inactive	37
Juveniles	**Joyce**	Socio-positive	39	Play	22
	Charles	Play	45	Socio-positive	29

For travelling behaviours, which included walking and excursions, juveniles showed the highest percentage (13.95%) followed by adult males (8.96%) and adult females (7.61%).

Five significant pair associations were identified among individuals (χ^2_{41}=1437.33; p<0.05, Table 8). Only the positive residuals of the association between individuals, expressed according to a Z-distribution, are displayed in Table 8, because they indicate associations between individual chimpanzees. The most significant associations (i.e. individuals most likely to associate with each other) occurred between Zoe: Daisy; Zoe: Charles and Daisy: Joyce (Z=3.29, p<0.001). Zoe was also likely to associate with Joyce (Z=2.58, p<0.01) and Daisy was also likely to associate with Lilly (Z=1.96; p< 0.05).

Table 8. Likelihood of chimpanzee individuals associating with each other more often than expected by chance.

Probability of associations	**Zoe**	**Amber**	**Lilly**	**Charles**	**Daisy**	**Joyce**	**Thabu**	**Yoda**
Likely **Z=1.96, $p<0.05$)**			Daisy		Lilly			
More likely **(Z=2.58, $p<0.01$)**	Joyce					Zoe		
Most likely **(Z=3.29, $p<0.001$)**	Daisy Charles			Zoe	Zoe Joyce	Daisy		

Discussion

This chapter of my study considered how chimpanzees in the Johannesburg Zoo utilised the available space in their enclosure and whether space use was influenced by the previous experience in restricted space. Subgroups were used for the evaluation of space use since chimpanzees tend to travel, forage and socialise in subgroups (Doran, 1997) within their home ranges that span from 11 km up to 340 km depending on the habitat (Yamagiwa, 1999). I expected the chimpanzees to utilise the enlarged, enriched area that was available to them more extensively as it has been suggested that complex environments will promote increased activity and will be utilized extensively (Clarke *et al.*, 1982; Perkins, 1992). However, I found that chimpanzees formed small subgroups significantly more frequently than large subgroups, and thus occupying a small portion, about 25% of the available space of 2500m^{2}, at any 1 point in time. One possible reason for the lack of use of a larger space is that the chimpanzees have been in this large enclosure for over 5 years and the novelty of the environment may have worn off. Celli *et al.* (2003) demonstrated that as animals become accustomed to available stimuli under normal conditions, the novelty of the stimuli wears off and the animals show a decrease in manipulation of the available objects and an increase in inactivity.

There was temporal consistency in subgroup space use, with subgroups remaining small more often than remaining large or changing from small to large and vice versa. There was also spatial consistency where subgroups tended to remain in any given area of the enclosure rather than moving between areas. The chimpanzees were utilising the entire enclosure, but they just tended to mostly remain in a chosen position within the enclosure as small subgroups that were the same size as their previous housing.

Subgroup formation was seasonally unvarying with the use of restricted space being the same in summer and winter. Subgroup formation was also unvarying under different weather conditions: chimpanzee subgroups restricted their space use on sunny, cloudy and overcast days. In free-living chimpanzees, there are differences in group movement patterns (Vedder, 1984), space use and composition in different seasons based on food availability (Doran, 1997). Since food availability in captive environments is predictably available, it is understandable that the chimpanzee subgroups would not show seasonal differences in space use; thus, other factors may be driving space use.

I also aimed to establish whether or not restricted space use was age/sex specific. All the chimpanzees were more likely to be part of a small subgroup rather than a large subgroup or not being part of a subgroup, with adult males not being part of any subgroups or participating in small subgroups significantly less than adult females and juveniles. This was unexpected as free-living female chimpanzees spend time foraging alone while males form close associations to defend territories (Williams *et al.*, 2002). Thus, I expected that adult females would be less spatially restricted than adult males and would be part of large subgroups or not part of any subgroups more often than adult males. A possible reason for this finding is that in captive environments males do not need to maintain specific territories as resources are not limited (since territorial behaviour is dependent on a predictable food supply; Zahavi, 1971; Kinnaird, 1992; Herbinger *et al.*, 2001), so forming groups to defend constantly available resources is not a necessity. This has been seen in Hawaiian Honeycreepers, *Vestiaria coccinea, Himatione sanguinea,* and *Loxops virens,* which ceased resource area defence when nectar was regionally superabundant (Carpenter, 1987).

With regard to females, captive adult female black spider monkeys, *Ateles fusciceps robustus*, which have very similar social patterns to chimpanzees, tend to form close associations with other females and their offspring, especially during periods of infant rearing, where females are likely to form clusters and associate with other females who have infants (Eisenberg, 1976). This may be of importance to my study as infants were present during my observations at the zoo.

I also predicted that juveniles would be less spatially restricted than adults. Since the juveniles were in the previous 10 m x 10 m enclosure for a much shorter time than the adults (with the youngest having been born in the enlarged enclosure), they would be less likely to show restrictions in their space use. Chimpanzees also display the highest activity levels as juveniles, displaying high levels of play behaviour (Palagi *et al.*, 2004), with adults showing high frequencies of inactivity (Videan, 2006). Juveniles would have associated with adult females (i.e. parental and alloparental care; Pusey, 1990), and most probably moved around with the females as a group; this could have potentially influenced my assessment of juvenile space use, as juvenile space use may have been affected by the presence of other individuals (i.e. social influences; Keeling and Duncan, 1989). Behaviour of individuals can influence subgroup formation and can affect how space is utilised. Therefore, I needed to consider social interactions as well as individual behaviours in order to evaluate my prediction, which will be discussed below.

Individual interactions may be an important determinant of how subgroups might move around the enclosure and how they utilise space, as particular individuals may follow others, whether it is following siblings, parents or potential mates (Sugiyama and Koman, 1979). Therefore, even though juveniles were part of small subgroups they also had the highest frequency of movement (walking and excursions) in the enclosure compared to adults. There was a high frequency of play seen in juveniles, which is expected, as play is seen predominantly in juvenile primates, facilitating physical and social development (Palagi, 2006). Play (especially locomotory play) can lead to greater space use, as individuals are moving around the available space. The greater frequency of movement coupled with the high frequency of play, led the juveniles to utilise more space than the adult males and females. However, while these trends in the data suggest that the juveniles were utilising more space within the enclosure than adults it still needs to be empirically tested with a larger juvenile sample size, which unfortunately was not possible in my study

My next aim was to ascertain the association between space use and behaviour. Activities of individuals can affect the distances between individuals and thus social spacing (Keeling and Duncan, 1991). There was support for my predictions with regard to space use and behaviour. Individuals that were not part of a subgroup and thus not spatially restricted displayed higher frequencies of non-restricting behaviours, such as walking, whereas spatially restricted individuals showed higher frequencies of spatially restricting behaviours, such as socio-positive behaviour. This is expected as socio-positive behaviour is associated with subgroup formation especially small subgroup formation as individuals can interact closely with one another. During social grooming sessions, the close contact of grooming would give rise to short inter-individual distances (McGrew and Tutin, 1978), and thus subgroups would utilise less space. All types of subgroups were characterised by high frequencies of inactivity and similar frequencies of play behaviour. These behaviours were ubiquitous across all subgroup types suggesting that they are not associated with any group size, regardless of group members or size. Inactivity does not require one to be part of a subgroup and it appears to not be a group dependent behaviour; so inactivity (which includes resting and sleeping) could result in an individual being left alone if the rest of the subgroup moves away, or could become part of a subgroup if other chimpanzees congregate around the solitary individual. Play behaviour could be characteristic of individuals that are part of any subgroup size as different forms of play behaviour can be associated with different subgroup sizes. Individuals playing in close contact with one another would be associated with small subgroup formation whereas individuals playing on their own may either be associated with large subgroup formation or they may be completely apart from a subgroup.

The final aim was to establish the association between space use and shade provided by trees or walls to assess whether chimpanzee space use was influenced by the presence of shade. Shade availability is an important resource as it reduces heat load and can alter behaviour as was seen in feedlot heifers, *Bos primigenius taurus*, (Mitlohner *et al.*, 2002). Shade could be a very important resource for captive chimpanzees, as their free-living counterparts live in dense forests that have high shade availability (Kosheleff and Anderson, 2009), and thus shade could influence chimpanzee space use and behaviour.

In order to determine whether restricted space use is influenced by shade availability I would have had to show: i) that space use is restricted mainly to shaded areas; ii) that there is no consistency of space use in different seasons, with greater space use occurring in Winter and more restricted space use in summer according to the relative importance of shade during these seasons; and iii) there should be no consistency in space use under different weather conditions, with greater use of space on overcast days (100% cloud cover) compared to sunny days (no cloud cover). If shade is a factor of restricted space use, the chimpanzees should not be in small subgroups on overcast days as there is no need for them to restrict themselves spatially.

I found that there was a greater use of shaded areas than sunny areas in the enclosure for the whole sampling period for all subgroup types. However, space use of subgroups was seasonally unvarying and did not differ under different weather conditions with small subgroups forming just as frequently on sunny as overcast days. Thus, shade would not be a possible factor of restricted space use as shade use was constant under all conditions with individuals remaining in small subgroups even when there was complete shade cover. However, this study has shown that shade is of importance to chimpanzees since the subgroups occupied areas in the shade far more often than areas in the sun. Therefore, even though reduced space use was not dependant on shade availability, chimpanzees selected areas based on the presence of shade.

Chapter 3

Experiment 2: Striped mice

Introduction

The African striped mouse, *Rhabdomys dilectus dilectus*, is a muroid rodent that is widely distributed throughout a variety of biomes within southern Africa (Skinner and Chimimba, 2005). Striped mice are terrestrial and diurnal with peaks of crepuscular activity (Perrin *et al.*, 2001). The striped mouse is an opportunistic omnivore, feeding mainly on grass seeds, and a high proportion of insects during the breeding season (Perrin *et al.*, 2001).

In the eastern mesic grasslands of South Africa, striped mice have a solitary lifestyle, in which both sexes have intra-sexually exclusive territories but male territories overlap several female territories and association between the sexes is restricted to mating (Schradin and Pillay, 2005b). Males in the grasslands have been found to have significantly larger home ranges (12446 ± 2000 m^2) than females (5760 ± 1098 m^2) (Schradin and Pillay, 2005b). Territories are maintained through aggression towards conspecifics (Perrin *et al.*, 2001).

Aims and predictions

In addition to the main aim of the study (Chapter 1), 3 more aspects of space use were considered for the striped mice. These are presented as 3 aims below together with specific question/predictions.

Aim 2: To determine the total movement of the striped mice by quantifying distance travelled to establish how space used by individuals relates to distance travelled.

Were individuals travelling longer or shorter distances in relation to the size of area they cover? The influence of previous restriction may be overridden if individuals travel long distances under natural conditions.

Aim 3: Establish space use of males and females to assess whether space use is sex specific.

I predicted that males would be less space-restricted than females, as females have been found to use less space than males in nature (Schradin and Pillay, 2004a).

Aim 4: Establish the space use of bold and shy striped mice to assess whether personality type (bold or shy) influences space use.

I expected that bold individuals would be less spatially restricted than shy individuals because bold individuals show greater levels of exploratory behaviours (Fraser *et al.*, 2001).

I tested these aims by comparing the space use behaviour of striped mice that were maintained in smaller ‘restricted’ housing with those maintained in a larger ‘non-restricted’ cage. In the following sections, “restricted” refers to individuals that were housed in the small Lab-o-tec^{TM} cages and control/“non-restricted” refers to individuals housed in the large 200 cm x 15 cm x 100 cm tanks.

Study subjects

For this study, 40 (20 male and 20 female) captive born (F1) striped mice were used, originating from a population in Pretoria (25º 40‶ S; 28º 30‶ E), South Africa. Bold and shy striped mice were identified prior to the experiment in order to obtain the appropriate sample size with an equal number of males and females that were bold and shy; there were 10 bold and 10 shy individuals per sex category (Personality tests are described in an Appendix). They were housed in the Milner Park Animal Unit, University of the Witwatersrand, under partially controlled environmental conditions 14L: 10D light: dark cycle (lights on at 05h00); 22ºC-24ºC and 30-60% rH. Subjects were bred in clear Lab-o-tec^{TM} cages (36.5 cm x 20.5 cm x 15cm; L x H x W). At weaning (16 days of age; Schradin and Pillay, 2004b), they were individually housed, as they are a solitary living species (Schradin and Pillay, 2005b), in Lab-o-tec^{TM} cages (36.5 cm x 20.5 cm x 15 cm). Each individual was provided with wood shavings as bedding and a handful of grass and shredded tissue paper as nesting material.

Individuals were also provided with a PVC nest-box (13 cm x 10 cm x 10 cm). Epol® mouse cubes and water were available *ad libitum*. Fresh fruit (apples, pears, paw paw) or vegetables (lettuce, carrots, broccoli) and mixed seed were provided daily per individual. A handful of nesting material and cardboard toilet rolls were provided bi-weekly for enrichment. Cages were cleaned every 2 weeks, and the cage contents replaced.

A control group of 40 (20 male and 20 female) F1 striped mice was also established, with 10 bold and 10 shy individuals per sex category. Individuals of the control group were bred in Lab-o-tec^{TM} cages (36.5 cm x 20.5 cm x 15 cm). At weaning (16 days old), the individuals that were being used as the control in my experiment were housed individually in large tanks (200 cm x 15 cm x cm 100 cm) with a surface area approximately 26 times greater than that of the Lab-o-tec^{TM} cages. These large tanks were provisioned in a similar manner to the restricted group in the Lab-o-tec^{TM} cages.

Sampling

After being restricted in the Lab-o-tec^{TM} cages or housed in large tanks for 60 days (individuals were 76 days old), the striped mice were placed individually into a test arena (tank measuring 200 cm x 15 cm x 100 cm). Striped mice were tested individually because they are solitary-living in nature. The base of the tank was covered with wood shavings and the tank was covered with a perforated lid to prevent the striped mice from escaping during video recording (see below) took place. The tank was cleaned with disinfectant soap and air-dried between tests to reduce carry-over odour effects. To minimise anxiety, the original housing cage was placed into the test arena, and the test subjects were allowed to enter into the test arena unaided. The control group was also video-recorded in the test arena, which was the same size as their home tank.

The behaviour of test subjects was video recorded with a Sony Handycam for 30 minutes between 08h00-12h00, as striped mice are most active during these times (Schradin, 2006) and no human observers were present in the room during recording time.

Space use recording of striped mice

At the end of the sampling sessions, the video recordings of the striped mice were used to trace the routes that each individual made between stops, i.e. every time an individual stopped moving, a tracing of the preceding route was made (Figure 8). This was done for 20 routes travelled per individual, 10 at the beginning of the filming session and 10 at the end of the filming session.

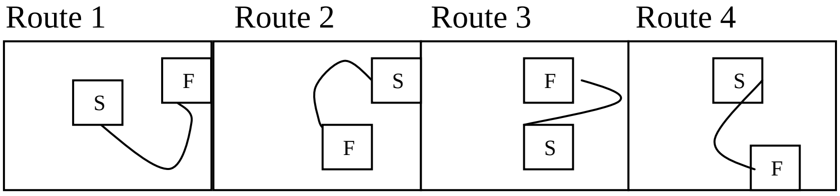


Figure 8. Diagrammatic representation of route tracings of the movement of individual striped mice. (S = point where a route starts; F = point where a route finishes)

The tracings were used to assess whether the individual movements were restricted to the size of the restricted housing. This was evaluated by placing a 375 mm x 215 mm (365 mm x 205 mm with 10 mm edge all around) grid, the size of the restricted cage, over each route, and the distance travelled was matched against 2 categories: within the 375 mm x 215 mm grid or greater than the 375 mm x 215 mm grid (Figure 9).

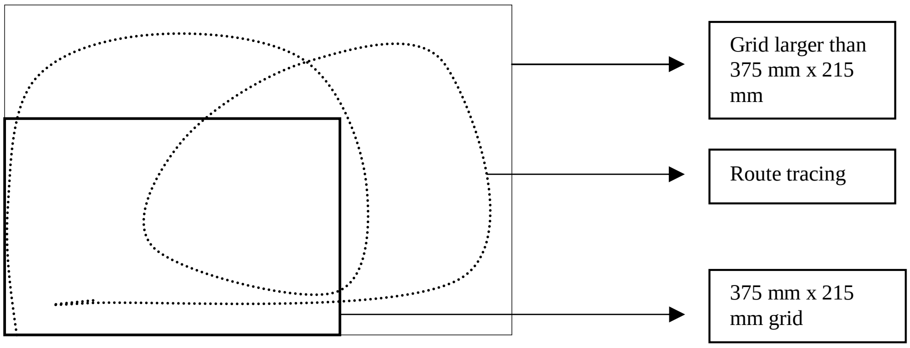


Figure 9. Diagrammatic representation of an example of how space use of a striped mouse route was evaluated.

This was different to how the chimpanzee space use was measured; the striped mice showed greater activity and continuous space use was sampled and thus distance could be measured whereas the chimpanzee space use was instantaneous sampling of a specific point in time.

The total distance that was travelled collectively per individual was also measured. The data collected were used to ascertain whether striped mice restricted their movements to an area the size of the smaller housing or whether their space use was unaffected by previous experience in restricted space. The data were also used to establish whether there were differences in space use for males and females and bold and shy individuals.

Data analysis

Space use and total distance travelled was analysed using a Generalized Linear Model analysis (GLZ) with a binomial distribution and probit link function, in which I tested differences in space use (restricted/non-restricted space use to the size of the original housing; response category) between sex and treatment (restricted and control).

An all effects model from the GLZ was used to ascertain which variables had a significant effect on the model output. Based on these results, appropriate first, second and/or third order effects were selected using user-defined protocols in the final model. Beta coefficients and confidence intervals (95%) were used to detect specific differences in the categorical variables when the Wald statistics for the effects were significant. GLZ analyses were run in Statistica version 6 (StatSoft, Inc. 2001). There was no difference between the first 10 routes and last 10 routes (Wald $\chi^2_1=0.80$; $p=0.370$) and these were pooled in the final analyses resulting in 20 routes per individual.

I next tested whether there were significant differences in space use and distance travelled (response variable) between sex (fixed factor: male or female) and personality (fixed factor: bold or shy), using a GLZ analysis, with the number of routes travelled coded as a covariate.

I further ran a regression analysis on the number of routes travelled and the total distance travelled for all individuals to assess the relationship between these 2 variables.

Experimental procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (clearance number 2006/94/03).

Results

Personality, sex and space restriction

There were significant differences in area covered for the restricted and control groups. Following the all effects model protocol, treatment, personality and treatment*sex were significant predictors of area covered in the final GLZ model (Table 9). Sex, personality*sex and treatment*personality were not significant predictors of area covered in the final GLZ model.

Table 9. Results from the GLZ tests analysing the space use of bold and shy females from control and restricted groups. p-values highlighted in bold are significant.

	Statistics results
Treatment	**Wald $\chi^2_1=435.81$; $p<0.001$**
Personality	**Wald $\chi^2_1=29.27$; $p<0.001$**
Sex	Wald $\chi^2_1=1.09$; $p=0.295$
Treatment*personality	Wald $\chi^2_1=0.17$; $p=0.682$
Treatment*sex	**Wald $\chi^2_1=7.61$; $p=0.005$**
Personality*sex	Wald $\chi^2_1=0.35$; $p=0.552$

For the treatment effect, the restricted group, regardless of sex and personality, limited their space use significantly more often than the control group (Figure 10). Shy individuals restricted their movements significantly more often than bold individuals.

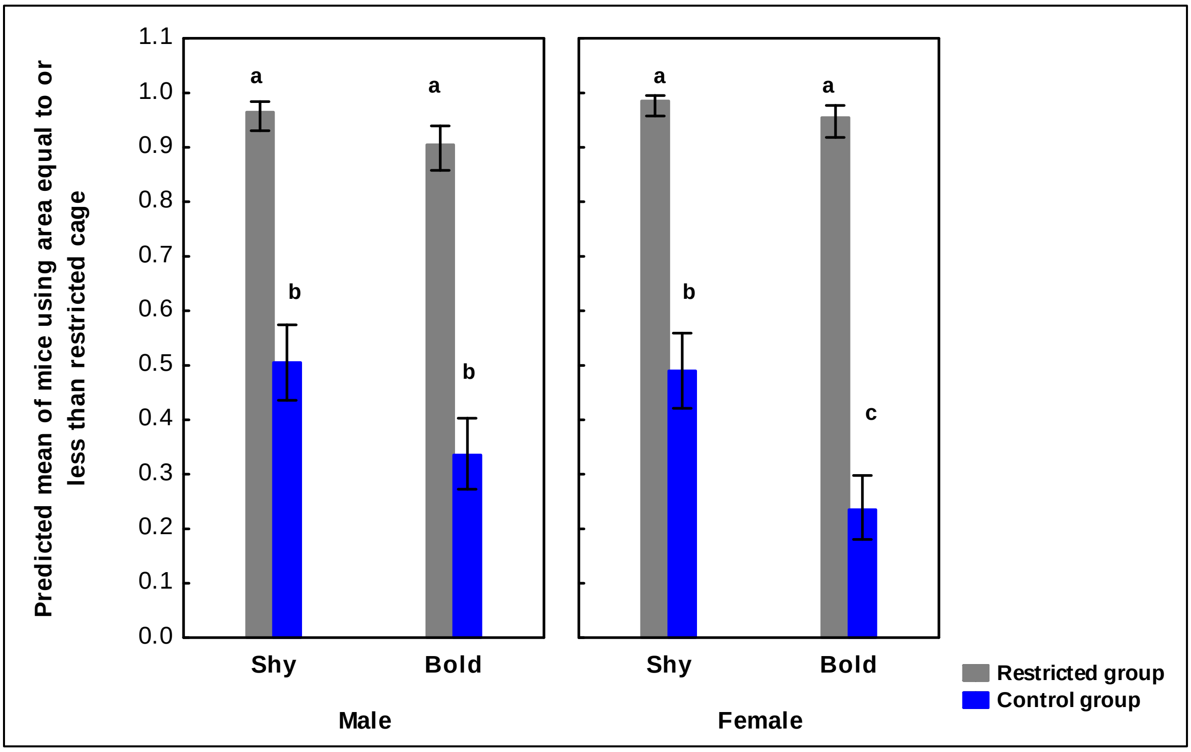


Figure 10. Predicted mean of distances covered by striped mice in an area less than or equal to the base area of the restricted housing. Bars with the same letters within each sex category are not significantly different. Whiskers denote standard error according to least squares means.

For the treatment*sex interaction, males and females from the experimental group restricted their movements more than the males and females from the control group, with males restricting their space use more than females in the control groups and females restricting their space more than males from the restricted group (Figure 10).

Distances travelled by striped mice

There were significant differences in distances travelled for the restricted and control groups. Following the all effects model protocol, the number of routes travelled, treatment, personality, sex, treatment*personality, treatment*sex and personality*sex were all significant predictors of distance travelled in the final GLZ model (Table 10). For the graphs of the distances travelled actual distance travelled was plotted, thus whiskers denote 95% confidence limits.

Table 10. Results from the GLZ analysing the distances travelled of bold and shy females from control and restricted groups. p-values highlighted in bold are significant.

	Statistics results
Number of routes travelled	**Wald χ^2_2=11540.74; p<0.001**
Treatment	**Wald χ^2_1=21069.27; p<0.001**
Personality	**Wald χ^2_1=649.92; p<0.001**
Sex	**Wald χ^2_1=242.38; p<0.001**
Treatment*personality	**Wald χ^2_1=253.16; p<0.001**
Treatment*sex	**Wald χ^2_1=1963.78; p<0.001**
Personality*sex	**Wald χ^2_1=197.40; p<0.001**

For the treatment effect, the restricted group travelled shorter distances compared to the control group (Figure 11). In the control group, the distances travelled out of an area the size of the restricted housing were significantly greater than the distances travelled within an area the size of the restricted housing. In other words, individuals were not confining the distances they travelled within the size of their previous housing. For the restricted group, the distances travelled within the size of the restricted housing were greater than the distances travelled out of the size of the restricted housing.

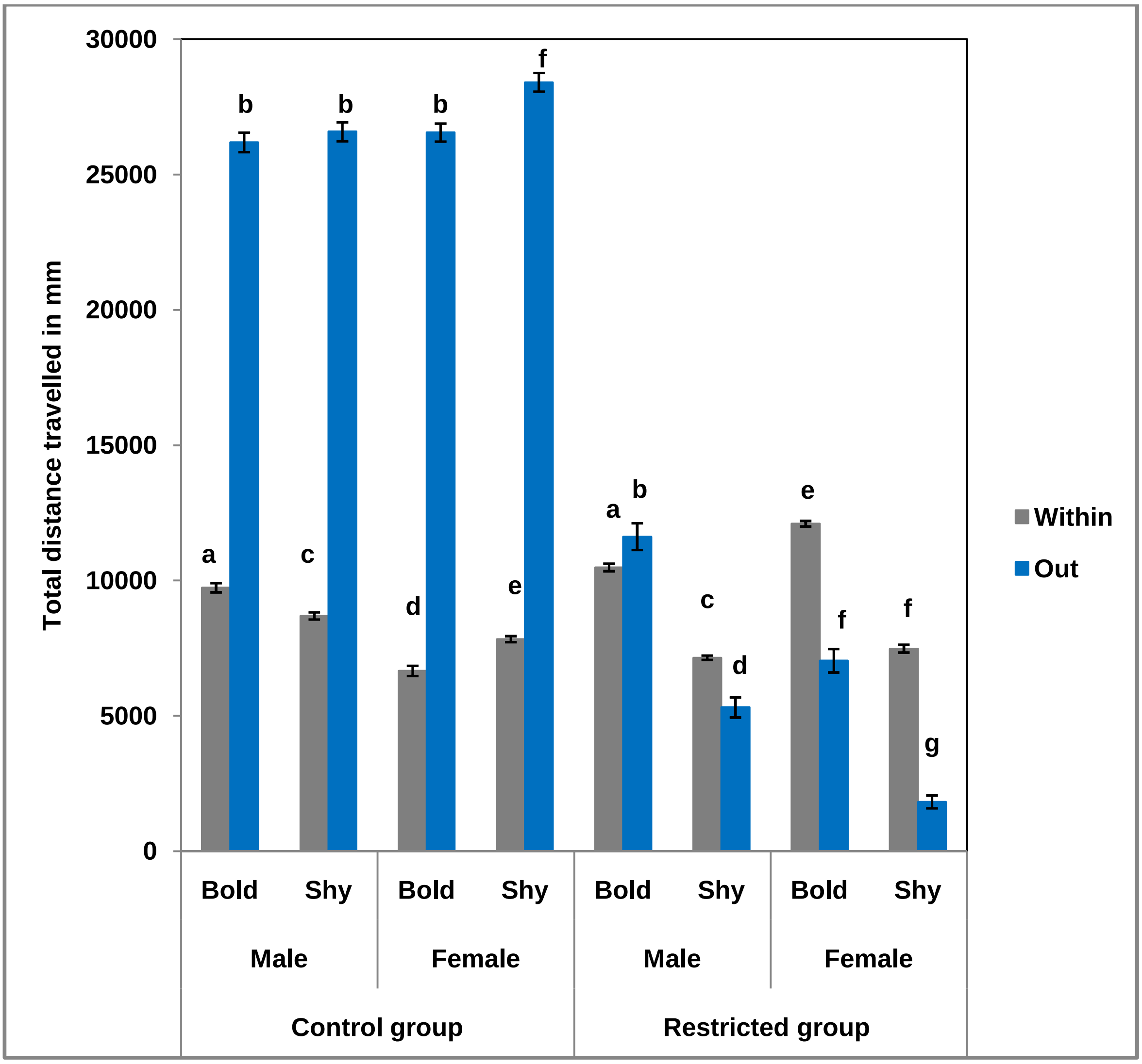


Figure 11. Total distance travelled within and beyond the area of the size of the restricted housing by individual striped mice from control and restricted groups. Bars with the same letters within each group (control and restricted) are not significantly different. Whiskers denote 95% confidence limits.

Distances and routes travelled

For the striped mice, there was a significant and strong positive relationship between the number of routes travelled and the total distance travelled (R^2=0.69; p<0.001; Figure 12). Individuals from the control group had the widest range of routes travelled and distance travelled. For the control, distances travelled out of the area of the size of the restricted housing were all above 1000 mm and the number of routes travelled was between 2 and 19 routes. The number of routes travelled within the size of the restricted housing was between 3 and 18 routes and the total distances travelled per individual were all less than1500 mm.

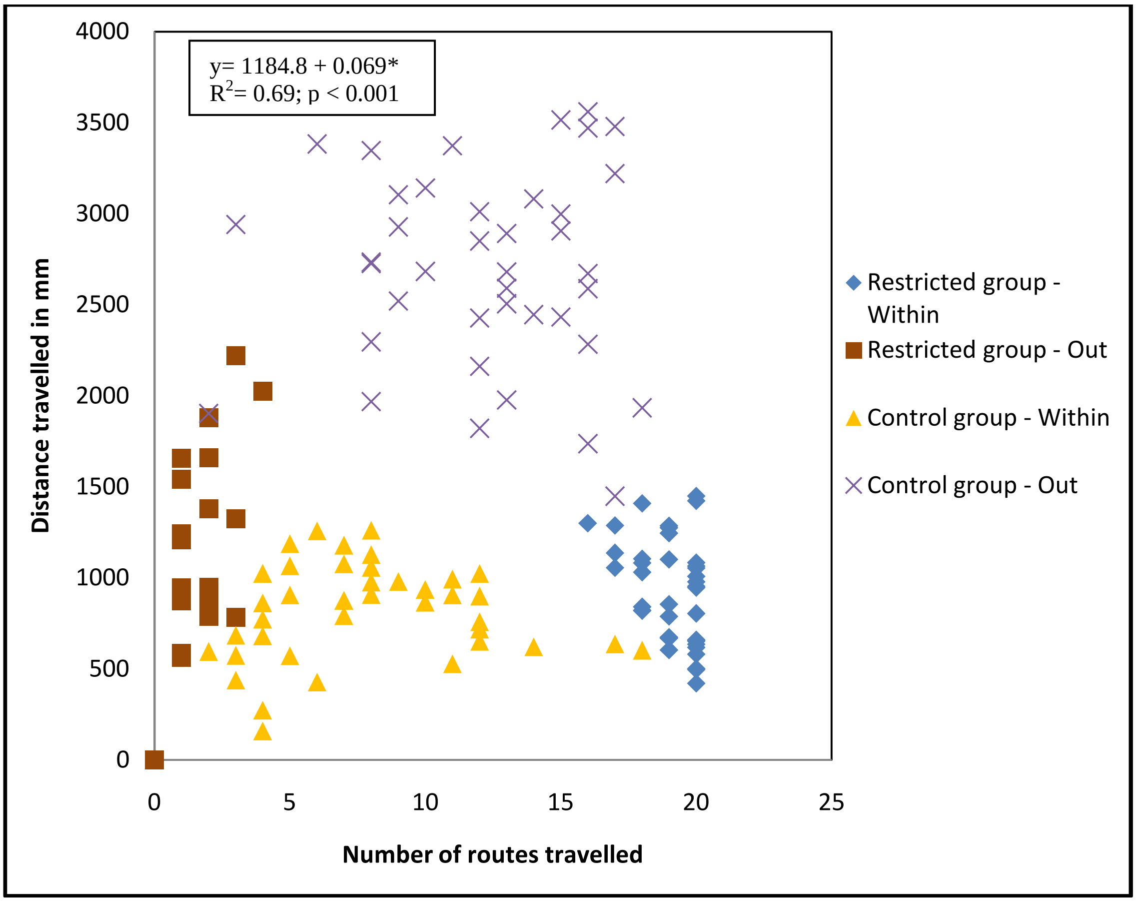


Figure 12. Distances travelled within and out of the area of the size of the restricted housing by individual striped mice from control and restricted groups in relation to the number of routes travelled per individual.

In comparison, for the restricted group, all the distances travelled within the area of the size of the restricted housing were between 1500 mm and 2500 mm, with individuals travelling between 15 and 20 routes (Figure 12). All the distances travelled out of the size of the restricted housing were below 2500 mm and individuals travelled between 0 and 4 routes.

Discussion

The second chapter of my study considered how spatial restrictions on striped mice would influence their subsequent space use in an enlarged area. Grassland *Rhabdomys* have a solitary lifestyle. Female and male home ranges are 5760 ± 1098 m^2 and 12446 ± 2000 m^2 respectively (Schradin and Pillay, 2005b). Therefore, the space use of striped mice was evaluated using individual movements rather than movements of a group. Overall, I found that prior spatial restriction did influence subsequent space use for striped mice in an enlarged area.

My first aim was to ascertain the space use of striped mice by quantifying the surface area used and thus establish whether they were restricting their movements to the size of the original, restricted housing. The restricted group limited their movements to the size of their old housing significantly more than the control group. Thus their experience in the restricted housing influenced their subsequent space use in an enlarged area. However, studies to date have not considered how restricting space use will affect subsequent space use.

My next aim was to quantify the distance travelled by the striped mice to establish how the space used related to the distances the individuals were travelling. For the control group, distance travelled was positively correlated to the area covered, long distances were travelled in routes that covered an area outside the size of the restricted housing and short distances were covered in routes that were within the size of the restricted housing. For the restricted group, a reversal of this pattern was observed, because there were longer distances for routes that covered an area within the size of the restricted housing compared to distances covering an area outside the size of the restricted housing. Thus, restricted individuals were travelling long distances but keeping these movements confined to the size of the original, restricted housing

Next I aimed to establish whether space use was sex specific. There were no differences in the space use between males and females, a finding that contrasted with my prediction that females would be more spatially restricted than males, as females have smaller home ranges (Schradin and Pillay, 2004b). However, male striped mice have been found to travel longer distances than females in captivity (Mackay, 2011). In my study, males travelled longer distances than females. Thus, my findings indicate that males had higher spatial restriction than females even though there were no sex differences in space use, as males travelled longer distances and females travelled shorter distances within similar space.

Finally, I aimed to establish the space use of bold and shy striped mice to assess whether personality types affect space use. It is known from the literature that bold individuals explore more than shy individuals (Fraser *et al.*, 2001; Rodel *et al.*, 2006), and thus I predicted that bold striped mice would be less spatially restricted than shy striped mice as they would travel further while exploring the new environment. There was a difference in space use for bold and shy striped mice, but there were no differences for bold and shy striped mice between treatments. Overall, bold striped mice travelled longer distances. There was a general decrease in distance travelled following restricted space for both bold and shy striped mice but the decrease in distance travelled was more pronounced for shy striped mice. Shy striped mice that were not previously restricted travelled longer distances than restricted and non-restricted bold mice. However, shy striped mice that had been restricted travelled the shortest distances compared to the restricted and non-restricted bold striped mice. Thus, the spatial restrictions affected shy striped mice more than bold striped mice with regard to the distances they travelled.

Chapter 4

Experiment 3: Common woodlice

Introduction

Common woodlouse biology

Woodlice, *Porcellio scaber* (Isopoda, Oniscidea), are terrestrial isopods (Edney, 1968). Woodlice inhabit mesic habitats (Hassall *et al.*, 2010) and are important detritivores, participating in the decomposition process of leaf litter (Zimmer and Topp, 1997).

Woodlice have cuticles that lack external waxy layers, making them sensitive to desiccation, and thus their survival is dependent on minimising water loss (Hassal *et al.*, 2010). Aggregation is important for minimising water loss and at low densities *P. scaber* spends time searching for other individuals with which to aggregate (Hassal *et al.*, 2005), and will also actively seek out moist shelters when posed with desiccating conditions (Hassal *et al.*, 2010). They are positively thigmotactic (touch) and negatively phototactic (light) under most conditions (Hughes, 1992).

Sensitivity to desiccation makes speed of movement and turn alternations important for woodlice to move away from unfavourable environments quickly (Morris, 1999). Although few studies have investigated the structure of the isopod brain (Warburg and Rosenberg, 1978), Kupfermann (1966) stated that turn alternations appeared to be mediated by some form of short-term memory. While there has been uncertainty about whether the memory mechanism is peripheral or central, Beale and Webster (1971) found that the differential activity of right and left legs was a sufficient condition for producing a strong bias in the direction of subsequent turns and thus concluded that a peripheral mechanism could not be discounted.

Aims

In addition to the main aim (Chapter 1), 2 further aspects were considered for space use in the woodlice. I have provided the aims and accompanying questions below.

Aim 2: To ascertain the total movement of the woodlice by quantifying distance travelled to establish how space used by individuals relates to distance travelled.

Will individual woodlice travel longer distances but still restrict their space use to the surface area of their old housing? The influence of previous restriction may be overridden because individuals travel long distances under natural conditions.

Aim 3: Establish space use of males and females to assess whether space use is sex specific.

Materials and methods

Study subjects

Restricted group

For this study, 40 woodlice (20 male and 20 female), with a size range between 10 mm - 15 mm, were collected from gardens in Johannesburg, South Africa and were placed in same-sex pairs, because they are a group living species and they tend to aggregate (Hassal *et al.*, 2005), in plastic circular bottles with a base area of 8 cm^2 and a height of 2cm. The bases of the bottles were covered with soil in order to maintain a more naturalistic environment. The woodlice were provided with leaf litter and carrot slices for food (D. Macullum 2010, pers. comm.). Dampened cotton wool was placed in the bottles to maintain a moist environment. The bottles were checked daily to ensure the woodlice had sufficient food and the cotton wool was moist. The bottles were covered with tin foil as woodlice generally live under rocks or logs where they are exposed to minimal sunlight; small holes were punctured into the foil to allow air to circulate in the bottles. The woodlice were kept in the plastic bottles for 14 days before they were used in experiments and video recorded (see below, page 53). All experiments were conducted in summer and all test subjects were exposed to ambient conditions in a laboratory at the University of the Witwatersrand.

Controls

A control group of 40 woodlice (20 male and 20 female) were also video recorded in the same manner as the restricted individuals. The woodlice for the control group were kept under the same conditions as the restricted individuals but in containers that had a base area of 154 cm^2 with 4 cm high walls.

Sampling

Two weeks after being housed in the 8 cm^2 housing (restricted group) and the 154 cm^2 housing (control group), the woodlice pairs were placed into a test arena 20 times the size of the restricted group housing, the same size as the control group housing. To minimise anxiety, the original bottles in which the restricted pairs were housed were placed into the arena, allowing the individuals to move into the arena unaided. For the control pairs, the original housing tub was tipped into the arena and individuals emerged into the arena unaided. Since the individuals were housed as pairs, they were filmed in pairs in the test arena (Figure 13). The arena had a base area of 154 cm^2 and the walls of the arena were 4 cm high. The walls were covered in Vaseline® to prevent the individuals from climbing up the sides, ensuring they remained within the test arena for the whole test time. A Perspex lid was placed on top of the arena as an added precaution to prevent test subjects from escaping. The floor of the arena was covered with soil and there were 3 plastic partitions to provide the woodlice with areas for thigmotaxis within the arena.

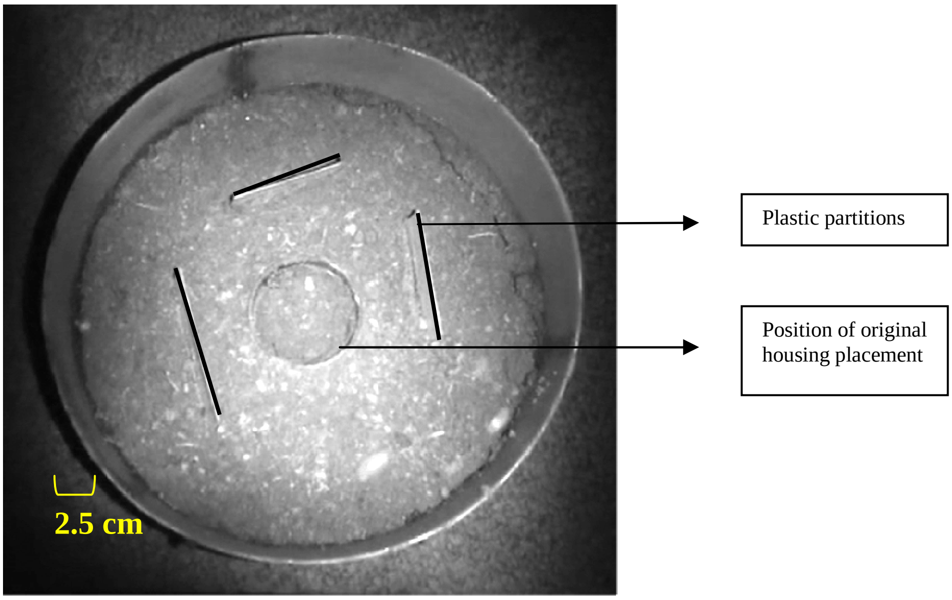


Figure 13. A photograph of an arena used to assess space use of woodlice

Each pair from the restricted and control group was placed in the arena and was marked with non-toxic, luminous yellow acrylic paint. Woodlice pairs were video-recorded with a Sony Handycam for 5 minutes in a dark room during night-time hours in summer, between 20:00 and 23:00, because woodlice are nocturnal and shy away from light (Cloudsley-Thompson, 1956). The paint aided in observing the individuals when being filmed using the night-shot setting on the camera.

In the following text, “restricted” refers to individuals that were housed in the small 8 cm^2 housing and control/“non-restricted” refers to individuals housed in the large 154 cm^2 housing.

Space use recording of woodlice

At the end of the sampling sessions, the video recordings of the woodlice were used to trace the routes that each individual made between stops. This was done for 20 routes travelled per individual, 10 at the beginning of the filming session and 10 at the end of the filming session. The same tracing techniques discussed for the striped mice were applied to the woodlice movements (Chapter 3, Figure 8). In the following text, 'movements' refers to the travelling of the woodlice.

The tracings were used to assess whether or not the individual movements of the woodlice were restricted to the size of their old housing in the restricted group. The area of the space use was evaluated by placing a circular grid, the size of the restricted housing, over each route, and the area covered was matched against 2 categories: within the 8.5 cm^2 (8 cm^2 with 1 mm edge effect) circle or greater than the 8.5 cm^2 circle (Figure 14). The total distance that was travelled per route per individual was also measured.

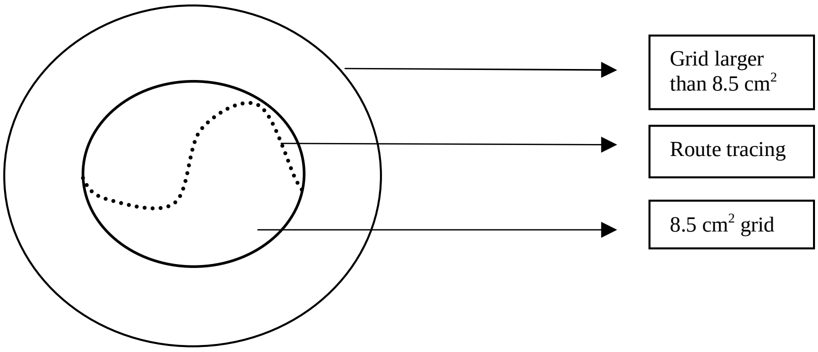


Figure 14. Diagrammatic representation of the way in which space use of each woodlouse route was evaluated.

These sampling techniques were applied to both the restricted and control group pairs to assess whether there were differences in movements of restricted and non-restricted individuals and whether exposure to restricted space limited movement in the test arena.

The data collected were used to ascertain whether woodlice restricted their movements to the area of the smaller housing or whether their space use was unaffected by previous experience in restricted space. The data were also used to establish whether there were differences in space use for males and females.

Data analysis

I used a Variance Components Analysis with an expected mean squares model to investigate whether individuals in a same-sex pair influenced one another's movements in the test arena. Treatment, sex and movements within and out the size of the restricted housing were fixed effects, individual was a random effect and distance and frequency (tested separately) were the dependent factors. Individual was not a significant predictor of distance (F_{40}=0.89; p=0.651) or frequency (F_{40}=0.98; p=0.516) of movement within and out the size of the restricted housing. Therefore, this predictor was not considered further.

Space use and total distance travelled for individuals were analysed using the same statistical analyses that were used for striped mice (Chapter 3). Analyses were run in Statistica version 6 (StatSoft, Inc. 2001). The first 10 routes and last 10 routes (Wald χ^2_1 = 0.25; p=0.615) were not significant predictors of the response variables in the final GLZ and these were pooled in the final analyses resulting in 20 routes per individual. I also tested whether space use and distance travelled (response category) differed between sex categories (categorical variable), with number of routes travelled coded as a covariate. I further ran a regression analysis on the number of routes travelled and the total distance travelled for all individuals, to assess the relationship between these 2 variables.

Results

Space use of male and female woodlice in control and treatment groups

There were differences in area covered for the restricted and control groups. Following the best subsets model protocol, treatment, sex and treatment*sex were significant predictors of the area covered in the final GLZ model (Table 11).

Table 11. Results from the GLZ analysis of the space use of male and female woodlice from control and restricted groups.

	Statistics results
Treatment	**Wald χ^2_1=10.74; p=0.001**
Sex	**Wald χ^2_1=9.08; p=0.015**
Treatment*sex	**Wald χ^2_1=4.53; p=0.036**

The restricted group restricted their movements more often than the control group (Figure 15). For the sex effect, males limited their movements to the size of their restricted housing more than females. For the treatment*sex interaction, males from the restricted group limited their movement significantly more often than males from the control group as well as females from both the control and restricted groups.

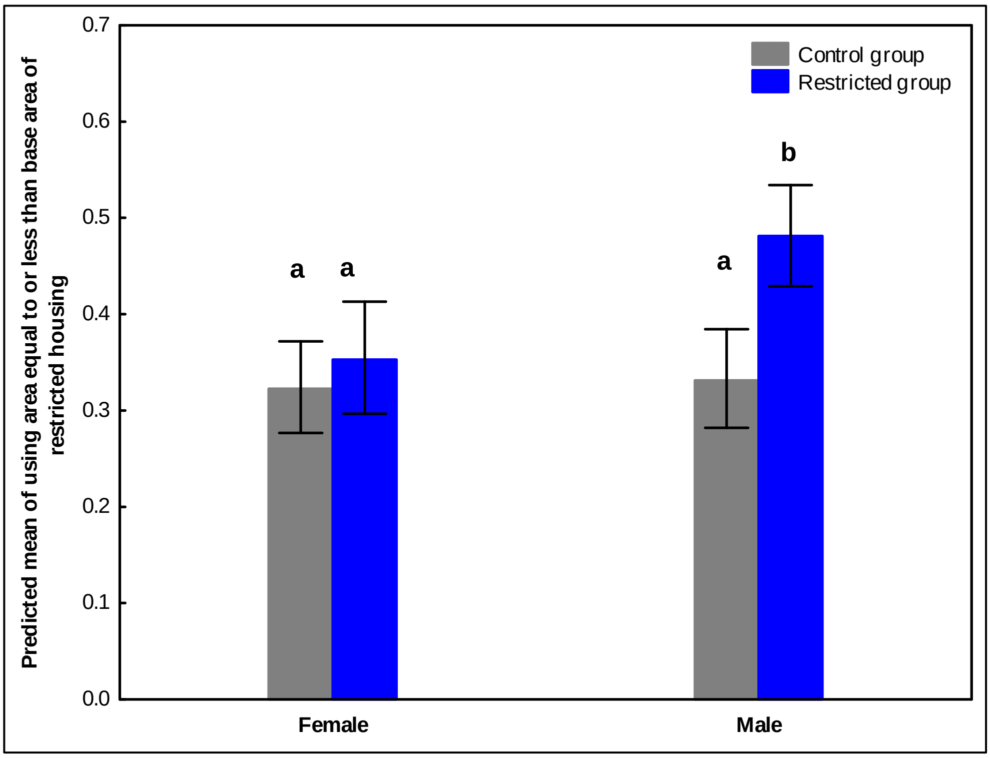


Figure 15. Predicted mean of woodlice movements covering an area less than or equal to the base area of the restricted housing. Bars with the same letters are not significantly different. Whiskers denote standard error according to least squares means.

Distances travelled by woodlice

There were no differences in distances travelled for the restricted and control groups. Following the all effects model protocol, the number of routes travelled, sex and treatment*sex were significant predictors of the distance travelled in the final GLZ model (Table 12). For the graphs of the distances travelled actual distance travelled was plotted thus whiskers denote 95% confidence limits.

Table 12. Results from the GLZ analysing the distance travelled by male and female woodlice from control and restricted groups. p-values highlighted in bold are significant.

	Statistics results
Distances travelled	Wald $\chi^2_1 = 0.50$; p=0.478
Number of routes travelled	**Wald $\chi^2_1 = 9204.36$; p<0.001**
Sex	**Wald $\chi^2_1 = 472.52$; p<0.001**
Treatment*sex	**Wald $\chi^2_1 = 836.02$; p<0.001**

For the sex effect, overall, females travelled longer distances than males. For the treatment*sex effect, females from the control group travelled significantly longer distances than all the other males and females (Figure 16). Males from the restricted and control groups travelled significantly longer distances than females from the restricted group. Distances travelled out of the size of the restricted housing for all groups were significantly greater than distances travelled within the size of the restricted housing.

Distances and routes travelled

There was a significant and strong positive relationship between the number of routes travelled and the total distance travelled ($R^2 = 0.60$; p<0.001; Figure 17). For the control and restricted groups, an increase in the number of routes was associated with an increase in the total distance travelled. Woodlice from the restricted and control groups travelled the shortest distances when they were within the size of the restricted housing and the longest distances when outside the size of the restricted housing.

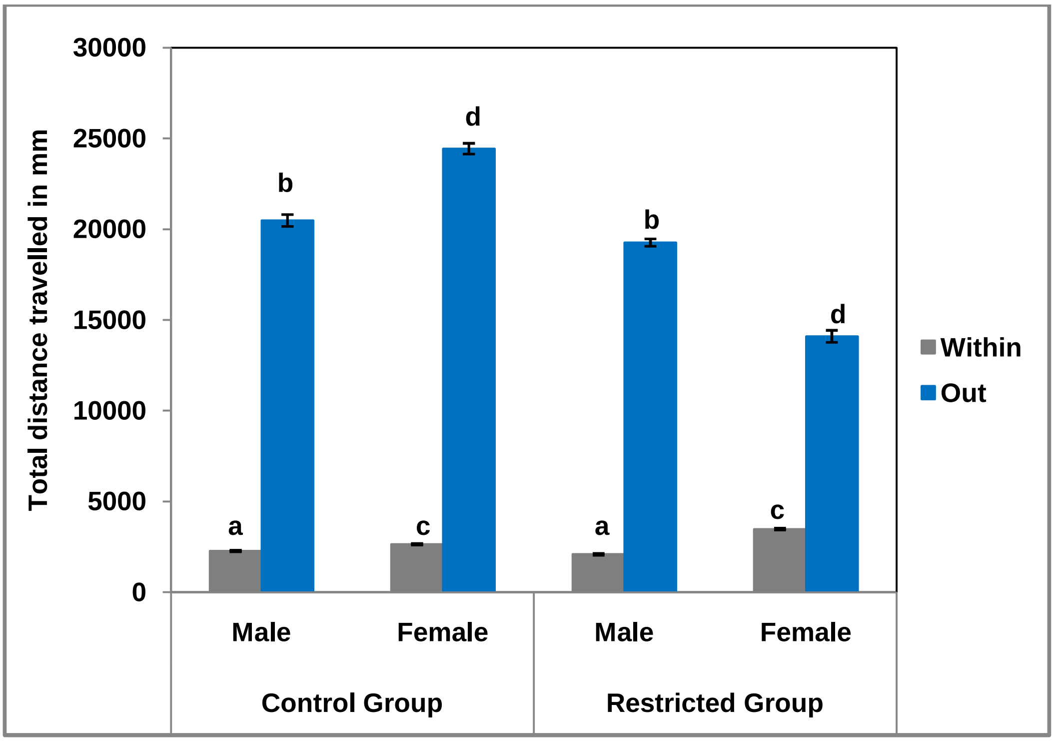


Figure 16. Total distance travelled within and out of the size of the restricted housing by individuals from control and restricted groups. Bars with the same letters within each group (control and restricted) are not significantly different. Whiskers denote 95% confidence limits.

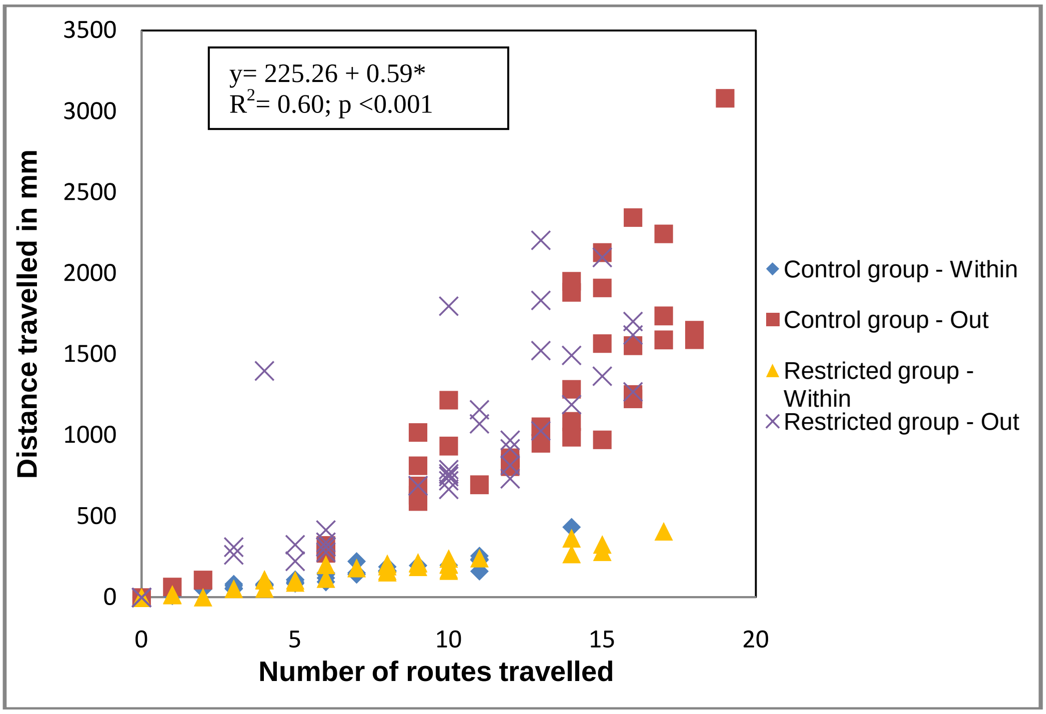


Figure 17. Distances travelled within and out of the area of the size of the restricted housing by individual woodlice from control and restricted groups in relation to the number of routes travelled per individual.

Discussion

I considered how spatial restrictions imposed on common woodlice would influence their subsequent space use in an enlarged area. Woodlice are very sensitive to desiccation and thus tend to aggregate with other individuals to minimise water loss (Hassal *et al.*, 2005). Since woodlice are generally found in close contact with other woodlice individuals, the woodlice in this experiment were housed and tested in pairs to attempt to mimic these natural, social conditions. Overall, I found that previous experience did influence subsequent space use in woodlice.

My first aim was to ascertain the space use of woodlice by quantifying the surface area used and thus establishing whether the woodlice were restricting their movements to the size of the original, restricted housing. Comparing space use between control individuals and spatially restricted individuals is the only (plausible) method of assessing space use in the woodlice of this study, since the distances woodlice travel in natural and captive environments is not known. Individual woodlice from the restricted group restricted their movements to the size of their old housing more often than the control individuals. Thus, the experience of woodlice individuals in the restricted housing influenced their subsequent space use.

My second aim was to quantify the distances that woodlice from restricted and control groups travelled to ascertain whether restricted space influences distances travelled in an enlarged area. Bayley *et al.* (1997) compared the locomotor behaviour of woodlice, *Oniscus asellus*, from contaminated sites with clean sites used as a control and found that woodlice from 5 control sites displayed a velocity, on a soil substrate, between 10.0 mm.s^{-1} and 12.9 mm.s^{-1} (I report velocity as Bayley *et al.* (1997) did not define how distance travelled by woodlice was measured). If equated to my project where the filming lasted 5 minutes, individuals that moved continuously would cover 3435 mm. This distance is almost 3 times the average distance travelled per individual from the restricted group (as well as the control group) in my study, so it would appear that distance travelled is being influenced by restricted housing. However, there were no significant differences in distances travelled between control and restricted groups. So while it is evident that in natural conditions, woodlice travel longer distances than seen in the individuals from my experiment, *O. asellus* individuals from the study by Bayley *et al.* (1997) were taken from the field and then tested within a few days, whereas the individuals from my experiment were kept for a long period of time in more restrictive environments than their counterparts found in natural environments. Additionally, the species used in the Bayley *et al*. (1997) experiment were different to the species used in my study, and the distances travelled may be species-specific. The woodlice in my experiment were only filmed at night whereas the woodlice in the Bayley *et al*. (1997) experiment were filmed in daylight hours, which could have influenced the speed that the photophobic woodlice ran (Morris, 1999).

My final aim was to establish space use of males and females to assess whether space use was sex specific. I did not expect to find any differences in space use for males and females because there have been no accounts of sex differences in literature. In terms of area covered, males from the restricted group were more restricted than those of the control group and all the females; males in the restricted group kept to within the confines of the size of the restricted housing more often. However, the restricted housing influenced the distances that females travelled more than males. While the distances travelled by restricted individuals were shorter than control individuals, females travelled the longest distances (control group) and the shortest distances (restricted group). So, even though restricted space did not influence subsequent space use in females, it influenced the distances they travelled, whereas males did not show a difference in distance travelled, only a difference in area covered. Thus confinement to restricted space could be said to influence male space use and female distances travelled.

Chapter 5

Experiment 4: German cockroaches

Introduction

The German cockroach, *Blattella germanica*, (Dictyoptera Blattelidae) is one of the most notorious pest species because it can survive well in any human habitation (Rivault, 1989). The German cockroach is omnivorous (Cloarec and Rivault, 1991), nocturnal, and prefers a moist and warm environment, making it a regular inhabitant of kitchens and bathrooms (Cornwell, 1968).

Shelter is an important resource for cockroaches (Deneubourg *et al.*, 2002) and thus accurate homing behaviour is important for cockroaches, so that they can return to shelters after foraging excursions. German cockroaches use idiothetic cues (information concerning an individual's orientation in an environment that is acquired by reference to a previous orientation of its body; Allaby, 1999), and learned visual cues to return to shelters after foraging (Durier and Rivault, 2000). Durier and Rivault (2001) found that German cockroaches learn the locations of specific resources in their home ranges and associate particular locations with specific resources, thus improving their foraging efficiency.

Cockroaches can also learn to avoid unpleasant situations. They are capable of associating a stimulus with punishment or reward, whereby they can be trained to avoid unpleasant situations by flexing their legs or remaining in lighted areas (which they would usually avoid) in order to avoid shock (Evans, 1984).

Male and female cockroaches differ in their occupancy of shelters. Gravid females do not eat and tend to stay in shelters until they deposit oothecae, and following this, start to feed again and may even accept a second mating (Rivault, 1989). Males are more mobile, spending the least amount of time in shelters and tend to hold a strategic place near receptive females (Rivault, 1989).

Aims and predictions

In addition to the main aim (Chapter 1), 2 further aspects were considered for space use in the cockroaches. I have provided the aims and accompanying questions/predictions below.

Aim 2: To ascertain the total movement of the cockroaches by quantifying distance travelled.

How does the space use of individuals relate to the distance they travel? Will individuals travel longer distances but still restrict their space use to the surface area of their old housing as was observed in woodlice and striped mice.

Aim 3: Establish space use of males and females to assess whether space use is sex specific.

I predicted that males would be more space restricted than females because males are found to disperse less (Bret and Ross, 1985) and do not travel over long distances (Rivault, 1989) compared to females.

Materials and methods

Study subjects

Restricted group

Cockroaches were obtained from South African National Standards (SANS) labs. Forty cockroaches (20 male and 20), with a size range between 15 mm – 20 mm, were used in experiments. The cockroaches were placed in same-sex pairs, since they are group living (Ame´ *et al.*, 2006), in plastic circular bottles with a base area of 8 cm^2 and a height of 2 cm. The bases of the bottles were covered with soil and the cockroaches were provided with Epol® mouse cubes, which had been crushed into a powder, for food and wet cotton wool for moisture, as suggested by Vincent Nell at SANS. The bottles were covered with mesh to allow air to circulate in the bottles. The bottles were checked daily to ensure the cockroaches had sufficient food and the cotton wool was moist. The cockroaches were kept in the plastic bottles for 2 weeks before being used in experiments. All experiments were conducted in Spring and all test subjects were exposed to ambient conditions in a laboratory at the University of the Witwatersrand.

Controls

A control group of 40 cockroaches (20 male and 20 female) were also video recorded in the same manner as the restricted individuals. The cockroaches for the control group were kept in the same conditions as the restricted individuals but in containers that had a base area of 154 cm^2 with 4 cm high walls.

Sampling

The same techniques that were used for sampling the space use of the woodlice were applied to the cockroaches. The same type of arena that was used during the filming of the space use in woodlice was also used for the cockroaches (Chapter 4, Figure 13). A pair of same-sex cockroaches was filmed in a dark room during night-time hours between 20:00 and 23:00, because cockroaches are nocturnal and shy away from light (Rivault and Durier, 2004).

In the following text, “restricted” refers to individuals that were housed in the small 8 cm^2 housing and control/“non-restricted” individuals refers to individuals housed in the large 154 cm^2 housing.

Space use recording of cockroaches

At the end of the sampling sessions, the video recordings of the cockroaches were used to trace the routes that each individual made between stops. The same tracing techniques discussed for the striped mice and woodlice were applied to the cockroach movements (Chapter 3, Figure 8).

The tracings were used to assess whether or not the individual movements of the cockroaches were restricted to the size of their old restricted housing. The same technique of area measurement that was used for the woodlice movements were applied to the cockroaches (see Chapter 4 Space use recordings of woodlice; Figure 14).

These sampling techniques were applied to both the restricted and control group pairs to assess whether there were differences in movements of cockroaches housed in restricted and non-restricted conditions and whether limited movement was influenced from being exposed to restricted space.

The data collected were used to ascertain whether cockroaches restricted their movements to the area of the smaller housing or whether their space use was unaffected by previous experience in restricted space. The data were also used to establish whether there were differences in space use for males and females.

Data analysis

I used a Variance Components Analysis with an expected mean squares model to investigate whether individuals in a same-sex pair influenced one another’s movements in the test arena. Treatment, sex and movements within and out the size of the restricted housing were fixed effects, individual was a random effect and distance and frequency (tested separately) were the dependent factors. Individual was not a significant predictor of distance

(F_{40}=24.39; p=0.516) or frequency (F_{40}=0.27; p=0.999) of movement within and out the size of the restricted housing. Therefore, this predictor was not considered further.

Space use and total distance travelled for individuals were analysed using the same statistical analyses that were used for striped mice and woodlice (Chapter 3 and 4). Analyses were run in Statistica version 6 (StatSoft, Inc. 2001). The first 10 routes and last 10 routes (Wald χ^2_1=0.14; p=0.706) were not significant predictors of the response variables in the final GLZ and these were pooled in the final analyses resulting in 20 routes per individual. I also tested whether space use and distance travelled (response category) differed between sex categories (categorical variable), with number of routes travelled coded as a covariate. I also ran a regression analysis on the number of routes travelled and the total distance travelled for all individuals, to assess the relationship between these 2 variables.

Results

Space use of male and female cockroaches

There were no differences in area covered for the restricted and control groups. Following the best subsets model protocol, treatment, sex and treatment*sex were not significant predictors of the area covered in the final GLZ model (Table 13).

Table 13. Results from the GLZ analysing space use of male and female cockroaches from control and restricted groups.

	Statistics results
Treatment	Wald χ^2_1=0.54; p=0.461
Sex	Wald χ^2_1=0.15; p=0.697
Treatment*sex	Wald χ^2_1=0.45; p=0.501

Distances travelled by cockroaches

There were significant differences in distances travelled for the restricted and control groups. Following the best subsets model protocol, the number of routes travelled, treatment and sex were significant predictors of distance travelled in the final GLZ model. For the graphs of the distances travelled actual distance travelled was plotted, thus whiskers denote 95% confidence limits.

Sex*treatment was not a significant predictor of distance travelled in the final GLZ model (Table 14). Beta estimates and confidence intervals (95%) revealed that for the treatment effect, overall, the restricted group travelled longer distances than the control group.

Table 14. Results from the GLZ analysing the distance travelled by male and female cockroaches from control and restricted groups. p-values highlighted in bold are significant.

	Statistics results
Number of routes travelled	**Wald $\chi^2_1 = 273.56$; $p<0.001$**
Treatment	**Wald $\chi^2_1 = 241.55$; $p<0.001$**
Sex	**Wald $\chi^2_1 = 2086.99$; $p<0.001$**
Sex*treatment	Wald $\chi^2_1 = 0.046$; $p=0.829$

The restricted group covered the shortest and longest distances when they were covering distances within and out of the size of the restricted housing, respectively (Figure 18). For the sex effect, females travelled longer distances than males. Females travelled the longest distances when they were covering distances out of the size of the restricted housing and males travelled the shortest distances when they were covering distances within the size of the restricted housing (Figure 18).

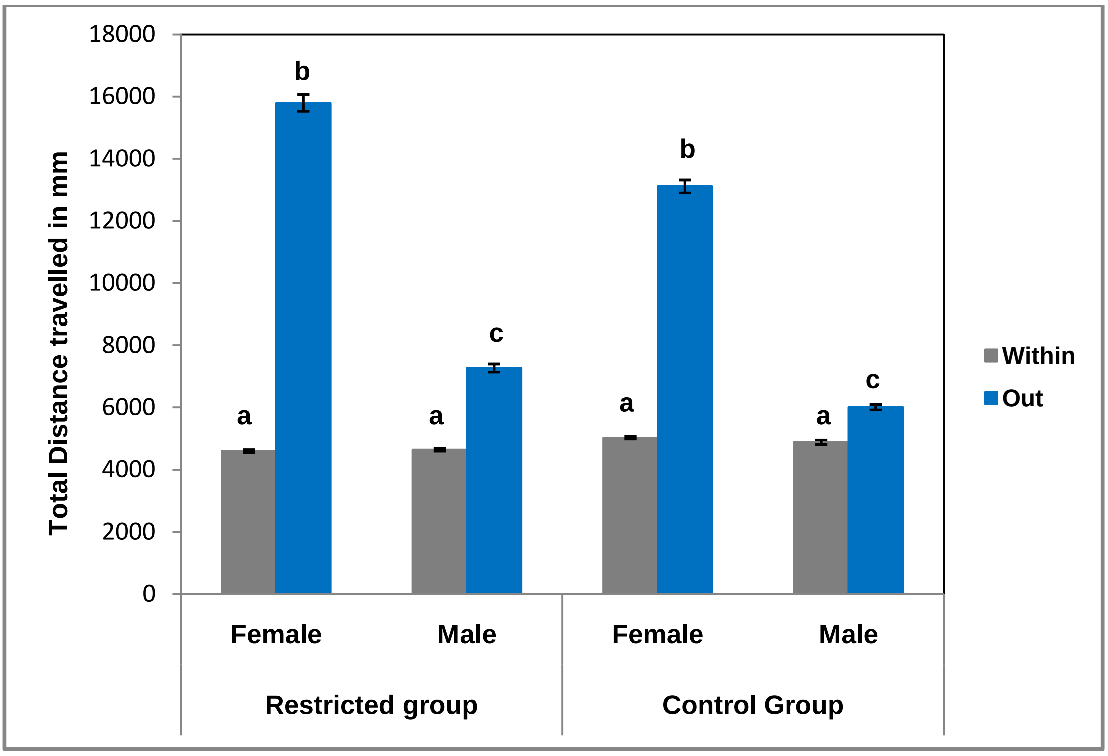


Figure 18. Total distance travelled within and out of the size of the restricted housing by individuals from control and restricted groups. Bars with the same letters within each group (control and restricted) are not significantly different. Whiskers denote 95% confidence limits.

Distances and routes travelled

There was a significant but weak positive relationship between the number of routes travelled and the total distance travelled ($R^2 = 0.34$; $p<0.001$; Figure 19). The distances and routes travelled within the area size of the restricted housing for the control and restricted groups were similar, with the total distances for both categories being below 750 mm (yellow triangles and blue diamonds in Figure 19). The distances covered out of the size of the restricted housing for the control and restricted groups were also similar to each other; an increase in routes travelled correlated to an increase in distance travelled.

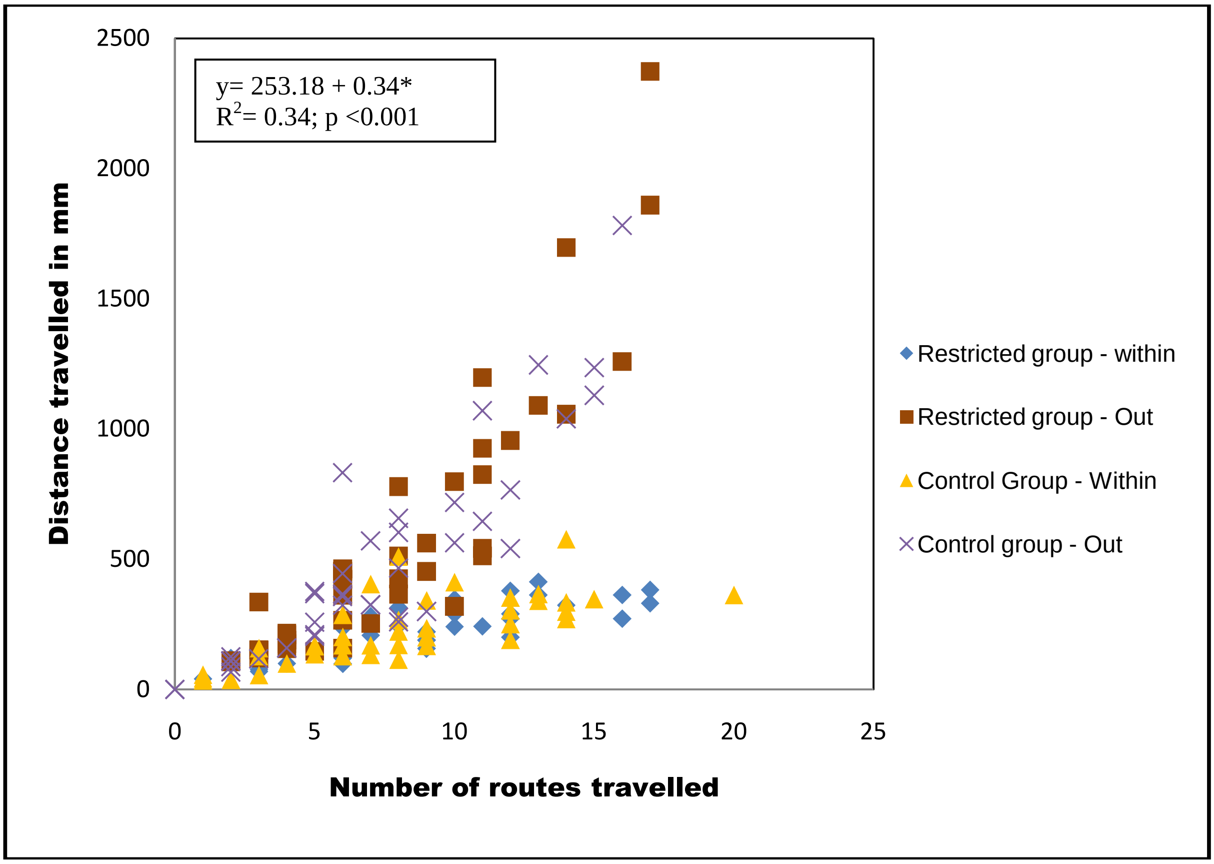


Figure 19. Distances travelled within and out of the size of the restricted housing by individual cockroaches from control and restricted groups in relation to the number of routes travelled per individual.

Discussion

My final experiment considered how spatial restrictions imposed on German cockroaches would influence their subsequent space use in an enlarged area. Cockroaches are group living (Ame´*et al.*, 2006), so I housed and filmed them in pairs. Jeanson *et al.* (2003) evaluated the movements of German cockroach larvae in a bounded space. They found that the average velocity along the periphery of the circular arena was 10.6 $mm.s^{-1}$. When equated to the time of my sampling (5 minutes), the individual cockroach would have travelled 3180 mm; this is more than 4 times the distance travelled by the restricted and control cockroaches in my experiment. However, the control and restricted individuals from my study were kept for a long period of time in restrictive environments whereas the individuals in the Jeanson *et al.* (2003) study had never been restricted at all. The study by Jeanson *et al.* (2003) showed that cockroaches do travel long distances when they have not been previously exposed to restrictive environments.

My first aim was to ascertain the space use of cockroaches by quantifying the surface area used. I found that there were no differences in space use between control and restricted individuals. These results were unexpected since exposure to restricted space has been shown to influence subsequent space use in an enlarged area in the other species that I studied (Chapters 2, 3 and 4) and I expected the restricted housing to have an effect on the subsequent space use of cockroaches in an enlarged area. Being exposed to restricted space does not appear to influence cockroach space use in an enlarged area.

However, when considering the total movements of the cockroaches (Aim 2), I found that overall, individuals from the restricted group travelled longer distances than the control group. This was also unexpected since there were no differences in area covered and if there was a difference in movement, I expected the restricted individuals to cover shorter distances in response to exposure to restricted space. Since cockroaches were not showing restrictions in their space use and previously restricted individuals were travelling longer distances than control individuals, the cockroaches' movements might reflect a rebound effect. The cockroaches increased their locomotion when given the opportunity to be in a larger environment. This resembles the findings of a study on rabbits, *Oryctolagus cuniculus*, which were transferred between pens of different sizes (Dixon *et al.*, 2010). When the rabbits were moved from small pens to larger pens they increased their activity levels thus showing a rebound effect with increasing activity when being exposed to greater available space (Dixon *et al.*, 2010).

My final aim was to establish the space use of males and females to assess whether there were sex differences in the space use of cockroaches. There were no differences in area covered but there were differences in distance travelled because females travelled longer distances than males. This concurred with my prediction because male cockroaches are found to disperse less (Bret and Ross, 1985) and travel shorter distances (Rivault, 1989) compared to female cockroaches.

Chapter 6

General discussion

To briefly recapitulate the findings of my study: space use in chimpanzee, striped mouse, woodlouse and cockroach test subjects was influenced by the previous experience of restricted housing in different ways. Chimpanzees restricted their inter-individual distances and striped mice and woodlice restricted their movements to the size of their previous, restricted housing. Conversely, cockroaches showed a rebound effect following exposure to restricted housing. In selected species, sex and personality effects were considered and comparisons to control groups and the effect of shade availability were used to determine the factors influencing spatially restricted movements. For the chimpanzees, shade availability, which would be the most likely explanation for restricted space use within the enclosure, was found to only influence spatial position and not the size of the space utilised. Other possible factors that could have been predictors of chimpanzee space use include the time of day, the maximum daily temperature, the percentage of available shade, the inter-individual distances, and the age-sex composition. In addition to group size not being random, however, these factors were found to not be good predictors of space use (Duncan, 2012). For the striped mice, woodlice and cockroaches the only variable that changed was the size of the enclosure they were exposed to. Since the striped mice and woodlice did restrict their movements to the size of their original housing, it appears that the previous experiences of these individuals were influencing their subsequent space use. This notion of previous experiences influencing later experiences is the foundation of learned helplessness which might explain the observed phenomena.

Learned helplessness

The learned helplessness hypothesis was proposed by Overmier and Seligman (1967) when they observed that after various rounds of inescapable shock treatments, dogs stopped trying to escape even after the shock treatments desisted. The learned helplessness effect is a passive response to aversive stimuli whereby the organism perceives that it has no personal control over the outcome of the situation, giving up after repeated failure (Santrock, 2002). There is the perception that the outcome is independent of the response since there is no personal control over the environment (Grimes, 1981). Passivity arises, where the motivation to regain control over a situation or to learn a new way of escape is lost (Barber, 1986). The organism “needs” to expect that the outcome is uncontrollable, since mere exposure will not have the same effect, i.e. an organism just being exposed to an uncontrollable situation will not show learned helplessness (Abramson *et al*., 1980). The organism needs to be exposed to an uncontrollable situation often enough that it comes to expect that the situation is uncontrollable. This expectation comes about from repeated punishment or failure to achieve a goal (Martinko and Gardner, 1982).

The learned helplessness effect has been observed in a variety of taxa, including mice, cats, rats, primates and fish (Maier and Seligman, 1976). There have even been accounts of the learned helplessness effect in isolated insect ganglia (Eisenstein and Carlson, 1997), suggesting that learned helplessness can occur in a variety of contexts. Learned helplessness has been studied largely in humans because of its medical importance. Learned helplessness is viewed as a sign of depression (Santrock, 2002), and has been widely used as a model for depression (Vollmayr and Henn, 2001). Behaviours associated with learned helplessness include passivity, inactivity, non-responsiveness and immobility (Eisenstein and Carlson, 1997). Therefore, if animals show high passivity or inactivity, they could be displaying learned helplessness as their behaviour does not allow for them to change their circumstances e.g. they do not realise they can move beyond a specific point as they have not attempted to approach that point.

At least 3 studies best demonstrate learned helplessness in animals. 1) Exposing rats, *Rattus norvegicus*, to uncontrollable tail shock resulted in them attempting to escape from an area, but when shock treatment desisted, the rats exhibited a deficit in learning to escape from escapable stress in future situations and also exhibited an exaggerated fear response (Greenwood *et al*., 2003). 2) Similarly, dogs, *Canis lupus familiaris*, exposed to shock treatment when they approached a specific area, stopped approaching the area even after shock treatments desisted (Grimes, 1981). 3) Beasor (2006) describes how pike, *Esox lucius*, that previously fed on guppies, *Poecilia reticulata*, and were then separated from the guppies with a glass sheet repeatedly struck the glass barrier, and eventually stopped approaching the guppies. When the barrier was removed, the pike still refrained from approaching the guppies. In all of these examples, animals were exposed to an initially uncontrollable situation. Once the situation had become controllable, the animals still continued to respond in the same manner as when the situation was uncontrollable.

Learned helplessness examples usually centre on animals receiving unpleasant, uncontrollable stimuli, such as the shock treatment mentioned in the first 2 examples. However, being exposed to an unpleasant stimulus may not be the only way for learned helplessness to develop. Maier (1980), even states that the situations do not necessarily need to be aversive; learned helplessness has occurred in situations with positive, negative and neutral stimuli. The important component of learned helplessness is that animals perceive that a situation is beyond their control and thus they inhibit their responses based on the expectancy that their actions yield no alternative outcome (Martinko and Gardner, 1982). Therefore, instead of receiving shock treatment to develop learned helplessness, one could be physically abused, fail school tests repeatedly or be exposed to a restricted environment. The important component is the controllability of the situation (Maier and Seligman, 1976).

I propose that the learned helplessness phenomenon could also be applied to animals in captive environments exposed to restricted space. Animals that have been exposed to a particular sized housing for a long time and are then moved to an enlarged area may not move beyond the size of the old housing even though there is more space available. If this occurs, the animals may be displaying learned helplessness, as they are not utilising the space beyond which they have known from their past, as was seen with white leghorn chickens and pike. If animals do show spatial restrictions in an enlarged area, would this phenomenon occur across a wide variety of captive species? Is learned helplessness in terms of space use related to neuronal complexity, so that species with high and low cognitive abilities show learned helplessness? If the expression of learned helplessness is not related to the cognitive levels of an animal, one would expect that animals with higher cognition, like mammals, and animals with lower cognition, like arthropods, would both display learned helplessness in terms of space use when introduced into an enlarged environment.

Learned helplessness and spatial learning

Song *et al.* (2006) investigated the effects of learned helplessness and chronic mild stress on the cognitive function of rats in a Morris water maze task, and found that learned helplessness and chronic mild stress significantly impaired spatial learning and memory. This was a consequence of up-regulation of plasma corticosterone concentration, and down-regulation of the hippocampal brain derived neurotrophic factor (BDNF) and cAMP-response element-binding protein (CREB) levels (Song *et al*., 2006). Changes with BDNF and CREB could lead to reduced hippocampal volume (Duman *et al.*, 2000) which is said to be correlated with a decline in verbal and visual memory (von Gunten *et al.*, 2000). A relationship between depression and spatial cognition was found in patients with Parkinson’s disease where only patients with depression symptoms had impaired working memory (Uekermann *et al.*, 2003).

Factors influencing the expression of learned helplessness

There were some inadequacies with the original learned helplessness hypothesis, since individual differences were not taken into account (Abramson *et al.*, 1980). The response to failure, especially in humans, is dependent on an individual's personality and level of self-esteem (Martinko and Gardner, 1982). It also depends on the reaction to failure and whether lack of success of an animal is attributed to internal or external factors (Grimes, 1981; Powell *et al.*, 1990). The reformulated theory of learned helplessness includes these attributes (Abramson *et al.*, 1989). Another consideration is the age of the animal, since young children have reduced susceptibility to learned helplessness in comparison to adults (Fincham and Cain, 1986).

Hellhammer *et al.* (1984) postulated that animals that are exposed to inescapable situations show a deficit in the subsequent acquisition of behavioural skills, due to acetylcholine-mediated inhibition of avoidance motivation and serotonin-mediated inhibition of behavioural activity. Hormones regulate the activity of cells and organs and thus contribute to the expression of specific behaviours (Solomon *et al.*, 1996). Hormones and neurotransmitters therefore need to be considered with regard to understanding the expression of learned helplessness. Clearly, those hormones and neurotransmitters related to stress and depression would be of interest, particularly uncontrollable stress (Weiss *et al.*, 1981; Maier and Watkins, 2005). Several hormones and neurotransmitters may be implicated including glucocorticoids, norepinephrine, acetylcholine, serotonin and dopamine (Checkly, 1996). Although I do not test hormone levels in my study, the relationship between hormones and various brain regions, like the hippocampus, is an important consideration since a captive environment provides a source of stress which can have an influence on the learning and memory of the study animals, and ultimately influence space use.

Learned helplessness in chimpanzees

When provided with more space in their new enclosure, the chimpanzee subgroups were found to restrict their space use to the size of their previous housing. Several factors were considered for the chimpanzee space use study, with shade availability being a possible major contributor to this use of restricted space. However, since shade was found to not be a predictor of chimpanzee restricted space use an alternative explanation could be learned helplessness. The learned helpless effect involves animals inhibiting their responses based on the expectation that their actions yield no alternative outcome (Martinko and Gardner, 1982). Therefore, the chimpanzees may be restricting their space use as a result of their previous experience in more restricted housing.

If learned helplessness is a predictor of space use then I would have expected chimpanzee subgroups to be: i) consistent in restricting their space use to 11m x 11m; ii) show seasonal consistency in space use; iii) show consistency of space use in different weather conditions; and iv) show a high frequency of inactivity (specifically the individuals in the sub-groups). In my study, all the predictions that were made for learned helplessness as a possible predictor of space use have been met. Space use by the chimpanzee subgroups within the enclosure was found to be consistently restricted to the size of their old housing; this is particularly important as the pattern of consistent spatially restricted subgroups appears to conform to the principles of learned helplessness (M. Seligman, 2010, pers. comm.).There was spatially and temporally restricted use of space in all seasons under all weather conditions, with a high occurrence of inactivity in adult males and females. The low levels of inactivity coupled with the greater occurrence of movement around the enclosure could suggest that juveniles are not showing learned helplessness to the same extent as the adults; this may support the idea that juveniles are less susceptible to learned helplessness compared to adults (Fincham and Cain, 1986). Inactivity has been singled out from the sampled behaviours as it is a behavioural marker of learned helplessness (Zhukov and Vinogradova, 2002).

Since the space usage of chimpanzees in the old enclosure was not known and there was no possibility to manipulate the enclosure of the chimpanzees, these predictions could support other explanations. Comparing space use in the old enclosure as well as the new enclosure could shed further light on space use following spatial restrictions.

Learned helplessness in striped mice

The movements of striped mice in an enlarged area were influenced by their experience in restricted housing. This could lend support to the idea of learned helplessness influencing space use of striped mice. Learned helplessness has been displayed in many rodents that have been exposed to aversive stimuli (Caldarone *et al.*, 2000; Chourbaji *et al.*, 2005) and rodents also are used as models of learned helplessness and depression (Edwards *et* *al.*, 2000; Yacoubi and Vaugeois, 2007). In my study, previously restricted individuals travelled long distances but confined these distances within the size of their previous housing. This lends further support to the idea of space use being linked to learned helplessness, since restricted individuals travelled longer distances within the confines of the size of the original housing, akin to moving within an invisible barrier, whereas non-restricted individuals did not keep their movements to within the confines of the size of the original housing.

Even though there were no sex differences in space use between male and female striped mice, males travelled longer distances within the size of the previous housing compared to the females, showing a more pronounced spatial restriction. Studies have found sex differences with regard to learned helplessness. Sex differences may be related to the species of study [e.g. humans (Shors and Leuner, 2003) and non-humans (e.g Wistar rats, Steenbergen *et al.*, 1990); human females are more susceptible to learned helplessness than human males, whereas the opposite occurs in male and female nonhuman animals.] Single or group housing (Palanza, 2001) or exposures to a single stress or repeated stressors (Kennett et al., 1986) are also predictors of sex differences. Female Sprague-Dawley rats are more resistant to single stressors but they fail to respond to repeated stressors, whereas the opposite occurs in males (Kennett *et al.*, 1986; Alonso *et al.*, 1991). Inescapable shock has stronger and more long lasting effects in male Wistar rats compared to females, with males having suppressed activity (Steenbergen *et al*., 1991).

Learned helplessness in woodlice

Individual woodlice from the restricted group restricted their movements to the size of their old housing more often than the control individuals. This lends support to the idea of learned helplessness affecting the space use of woodlice, as the experience of restricted housing conditions influenced space use in a larger area. There have not been any studies on learned helplessness in woodlice nor are there many studies investigating the space use of woodlice, so it is difficult to quantify the movements of woodlice in normal circumstances. However, the study on the *Chasmagnathus* crab by Tomsic *et al.* (2003) mentioned previously (Chapter 1) and a study by Johnson (1977) on individual recognition in banded shrimp, *Stenopus hispidus,* suggests that crustaceans are able to learn and retain memories to some extent. Thus, it may be possible for woodlice to 'remember' being in restricted space. Woodlice, *Armadillidium vulgare*, have shown the ability to display new, problem solving behaviours when faced with difficult situations (Moriyama, 2004), suggesting that they possibly have the ability to learn from the consequences of previous behaviours.

Since woodlice from the control and restricted groups originated from the exact same conditions, with the only difference being housing size in captivity, it seems plausible to say that previous experiences can affect subsequent space use in woodlice and that they can show learned helplessness. The possible presence of learned helplessness in woodlice suggests that learned helplessness in terms of space use can occur in arthropods as well as mammals.

Absence of learned helplessness effect

When exposed to an enlarged environment, the cockroaches did not restrict their movement. The cockroach movements seemed to reflect a rebound effect by increasing their locomotion when presented with more space. A possible reason (other than a rebound effect) why cockroaches did not display learned helplessness is that cockroaches were not reared in restricted spaces, so there is a possibility that developmentally they had passed a stage (i.e. sensitive period),whereby the spatial environment is likely to influence their future spatial perceptions. A classical example of the influence that an early environment has on the perception of future situations has been shown in kittens, *Felis catus*, where those that had been reared in the dark at different ages were placed in a stationary cylinder covered by a rotating drum with black and white stripes, showed effects of different types of visual deprivation (Daw and Wyatt, 1976).

If the spatial environment does influence future spatial perceptions in cockroaches, future studies could manipulate the age of the cockroaches used, to evaluate at what age cockroaches need to be confined in order to show learned helplessness. Additionally the holding time in restricted space could also be manipulated, to investigate how long an animal needs to be exposed to restricted space in order to develop learned helplessness; this would be applicable to all the species tested. Woodlice may not have been similarly affected as cockroaches as the longevity of specific development stages would differ from cockroaches because of the inherent differences in their life history biology which is discussed below.

Is learned helplessness evident?

Few studies have examined how animals utilise and cope with more space, especially in captive environments (Marriott and Meyer, 2005). The focus of space utilization research on captive environments has mainly been on animal reactions to decreases in available space (Coelho and Bromblett, 1981; Caws and Aureli, 2003) or it has focused on the effect of enrichment on animal space use by increasing enclosure complexity (Odberg, 1987; Schapiro and Bloomsmith, 1994). While a decrease in available space is unfavourable for good welfare and an increase in available space is viewed as enrichment for many species, the utilisation of the greater available space may be dependent on previous experiences. If this is the case, it is important to consider how an animal's previous experience in a more spatially restricted environment will affect its subsequent space use when provided with more space.

My study has shown that previous experiences in more spatially restricted environments do affect subsequent space use, where animals will restrict their movements and spacing to the size of their original restricted housing. Since shade availability was not a factor influencing chimpanzee inter-individual distances and restricted striped mice and woodlice individuals restricted their movements to the size of their original housing more than control individuals, learned helplessness seems the most plausible explanation for restricted movements. Though learned helplessness studies have not focused on animal space use, the design of a captive environment is comparable to the environments that psychologists used to generate learned helpless behaviour; they are designed to prevent attempts at escape (McBride, 1984). This was shown in pike and white leghorn chickens that were discussed in Chapter 1. The pike and white leghorn chicken examples demonstrated that when animals have been previously restricted and are given the opportunity to escape they may fail to do so as they perceive that they are not able to move beyond a specific point. The spatial restrictions of these 2 examples are slightly different to the spatial restrictions shown in my study. In the white leghorn chicken and pike, individuals did not move beyond the point where a barrier was previously located. In my study, individuals moved around all the available space, but they just kept their movements, or inter-individual distances, restricted to the size of the previous housing.

While learned helplessness appears to be the most plausible explanation for restricting subsequent space use, how can we be certain the animals were not just restricting their space use to areas that would occur in nature, particularly the chimpanzees? This can be answered by examining more closely the space use in nature. Chimpanzees are a group-living species that tend to form subgroups naturally, so how would one separate natural subgroup formation from learned helplessness? The first consideration is that subgroups in nature consist of individuals that are much further apart than those I observed in these captive chimpanzees. Wrangham and Smuts (1980) consider subgroups to be chimpanzees within 100m of each other, and therefore any individuals that were less than or equal to 100m away from another would form part of the same subgroup. The chimpanzees in the zoo can be widely spaced since in natural conditions they use vast areas and the current zoo environment provides the space for a wide distribution; there was enough space in the enclosure for individuals to spread themselves out considerably, with about 312m^2 of space per chimpanzee and food was scattered within the enclosure to encourage foraging over wide areas. However, my findings showed that while the chimpanzees at the zoo had the opportunity to be widely distributed, they were more likely to be part of a subgroup (individuals within 11m of each other), staying in much closer proximity to each other than seen in nature; furthermore, it is unusual for chimpanzees to remain close together in captivity (J. Goodall 2011, pers comm.)"

The second point that needs to be considered is when individual chimpanzees occurred on their own. If chimpanzees are often on their own and not part of a subgroup, how can we tell whether learned helplessness is being displayed because being far apart from other individuals suggests that learned helplessness is not being displayed, because I have defined the expression of learned helplessness in terms of on the occurrence of chimpanzees being closely located to each other? This can be answered by considering how chimpanzee subgroups are restricting their space use. For the chimpanzees, restricted space use is a *group space* phenomenon where individuals within a subgroup are performing activities within an imaginary "barrier"; in this case a "barrier" of 11m x 11m.

The boundary of the "barrier" is determined by social group spacing with the total area occupied being determined by all the individuals within the subgroup. The hypothesis of learned helplessness is supported if social subgroups remain within the bounded space. By my interpretation of learned helplessness, the chimpanzee subgroups do not need to remain in the exact same area over time, as long as they displayed restricted space use while travelling around the enclosure. Subgroup cohesion can be associated with behaviours that do not require movement over space, such as inactivity and social grooming, whereas subgroup fission can be associated with behaviours that require movement like walking (Lehmann *et al.*, 2007), in which case perceived "barriers" will be "broken down". My findings showed that individuals that were part of a subgroup, more frequently displayed behaviours that were associated with subgroup cohesions, like socio-positive behaviour, and individuals that were not part of a subgroup more frequently displayed behaviours that were associated with subgroup fission, like walking. Whether chimpanzees perceive restrictions as an individual effect as well as a group effect remains to be tested since the results from the striped mice and woodlice (Chapters 3 and 4) suggest that it can also be an individual effect. Therefore, individual chimpanzees sitting or performing activities on their own would be within their own 11m x 11m “barrier” as they would be perceiving space on an individual basis, as was tested and shown in the woodlice and striped mice.

The same concept that was discussed for the chimpanzees applies to the striped mice and woodlice, where there would be the perception of a “barrier”. For these species tested, the perception of a “barrier” would be an *individual space* phenomenon and not a group space phenomenon since striped mice were individually housed and tested and the woodlice individuals were not influencing each other’s movements i.e. there was no group effect. The single movement an individual made (path moved between stops) occurred within a perceived barrier, and therefore the distances they travelled between stops were limited to the size of their original, spatially restricted housing.

Though it is evident that the space use of the captive chimpanzee subgroups is much more restricted than their natural counterparts, it is more difficult to determine whether the movements of the striped mice, woodlice and cockroaches are more restricted than their natural counterparts. Individual movements that animals make between stops are not widely studied, and for this reason the control groups used in the experiments with striped mouse, woodlouse and cockroach experiments were the best way to evaluate whether there was this perception of a “barrier”. Since the striped mice and woodlice from the treatment group did restrict their individual movements significantly more than the control group, it seems plausible to assume that the restricted individuals in essence perceive a “barrier” and restrict their movements accordingly by halting their movements when they reach the imagined “edge”.

Perceived loss of control is the underlying basis of learned helplessness (Baum *et al.*, 1986), and as a result memory and learning of an individual can be compromised (Song *et al.*, 2006). However, if an individual is displaying learned helplessness, it would have to remember a previous suffering (stressor) in the first place. In my study, the test species would have to have an altered perception of space or some form of memory of being restricted in order to remain restricted in the enlarged area. The perception of available space would be based on the memory of previous experience; in this case, the animals remember not having the ability of moving further than a specific distance. Therefore, this could be a self-perpetuating phenomenon where memory leads to restricted space use, and these restrictions then have adverse effects on the animal’s memory, thus reinforcing the spatial restricting behaviour. Memory ultimately ends up being altered by the behaviour it helped generate.

An alternative consideration for restricted space use is habit formation. Wolpe (1968) discussed how cats, *Felis catus,* that were exposed to shock treatment developed a permanent habit of anxiety responses. They displayed these neurotic anxiety-response habits in their shock-cages as well as rooms that looked similar to the rooms where the shock treatments were performed. Even after the shock treatments desisted, the cats did not show any weakening of anxiety. The same can be applied to the 3 captive species of my experiment that have been exposed to a new environment, yet still maintained their use of restricted space that they experienced previously. Wolpe's (1968) study relates to learned helplessness yet also leads to the idea of habit formation. Habits can form, or be triggered, based on the context of a situation where they would be controlled by antecedent stimuli (Yin and Knowlton, 2006); in my study, this would be restricted space. The chimpanzees, striped mice and woodlice may have developed the habit of using restricted space based on the experience in smaller housing.

There is still much uncertainty regarding the detailed mechanisms that underlie habit formation but there are attempts at trying to understand how synaptic plasticity in basal ganglia alters the output of neural networks (Yin and Knowlton, 2006). One of the principal differences between habit formation and learned helplessness is that a habit can be easily created and broken (Holland *et al.*, 2006), whereas learned helplessness deals with more permanent changes in brain function (Weiss *et al.*, 1981). Learned helplessness is a cognitive function of expectations about the environment (Overmier, 2002), and is associated with changes in hormone levels arising from stressful situations (Checkly, 1996). The chimpanzees had been in the enlarged enclosure for almost 5 years by the time my study took place. If group spacing was as a result of habit formation, it would be expected that the habit would most likely have been broken after such a long time of being exposed to an enlarged enclosure. Whether the woodlice and striped mice are restricting movements as a result of habit formation would need to be further tested as they were not exposed to the new, enlarged area for a long time before the experiment was conducted.

Many studies have shown that learned helplessness is accompanied by changes in the serotonergic system (Dwivedi *et al.*, 2005) with a profound depletion of serotonin (Petty *et al.*, 1994) and an elevation of corticosterone levels (Dwivedi *et al.*, 2005; Song *et al.*, 2006). Whether the hormones are the drivers of change or as a consequence of learned helplessness is not clear, but there is an obvious association between the two, such that several classes of anti-depressant drugs can reverse learned helplessness (Sherman *et al.*, 1982). Additionally, voluntary freewheel running has been found to decrease the behavioural effects of uncontrollable stress in Sprague Dawley rats (Greenwood *et al.*, 2003), and social buffering has been found to decrease glucocorticoid responses in many social species by moderating the Hypothalamic-Pituitary-Adrenocortical (HPA) system which is sensitive to stressful situations like perceived loss of control (Hennessy *et al.*, 2009), which is the underlying basis of learned helplessness (Baum *et al.*, 1986). The underlying neuro-endocrine system needs to be examined in order to confirm whether the space use restrictions are as a result of learned helplessness rather than habit formation.

Is learned helplessness related to neuronal complexity?

My study has shown that a variety of species can display learned helplessness but I further question whether learned helplessness is dependent on neuronal complexity, i.e. do mammals and arthropods of varying neuronal complexity all show learned helplessness? Sporns (2003) defined complexity as a degree to which a neuronal system integrates specialised information and a structural network produces a pattern of functional interactions. Another definition of complexity is the number of distinguishable components, which would range from the anatomical components to behavioural components (i.e. physiologically distinct processes and behaviourally distinct perceptions; Bullock, 2002). For the purposes of this study, neural complexity will refer to the cognitive ability of the test species in relation to the other 3 test species - chimpanzees are considered to have the highest cognitive ability as chimpanzees display very advanced cognitive abilities (Byrne and Whiten, 1992; Hare and Tomasello, 2004), followed by striped mice and finally woodlice and cockroaches which have the lowest cognitive ability, since complex cognition in arthropods is said to be rare (Maclaurin, 1998) and arthropods display less complex behaviour than mammals (Mizunami *et al.*, 1999). Mizunami *et al.* (2004) compared the functional characteristics of the arthropod and mammalian brain. Speed and economy were a priority of information processing for the arthropod brain, whereas precise and flexible information processing was a priority for the mammalian brain. For this reason, the species chosen were selected because of their distinct neuronal complexity in order to test whether or not learned helplessness is related to neuronal complexity.

Chimpanzees (97%) and striped mice (95.25%) showed a markedly reduced space use following restrictions (percentages indicate the occurrence of restricted space use in the total sampled). Woodlice (35.28%) also showed restricted space use following experience in restricted housing. While it may appear that woodlice do not show spatial restrictions since the percentage of restricted space use for woodlice is much lower than the chimpanzees and striped mice, it needs to be considered that there was a significant difference in space use between control and restricted woodlice, indicating their space use was influenced by previous restrictions. This indicates that space restriction and learned helplessness is not an all or nothing effect depending on neuronal complexity but may be graded according to neuronal complexity, since the 2 mammal species seem to display it more markedly than arthropods. I say this even though the cockroaches displayed a rebound effect to restricted housing, which may be a species-specific reaction. It is interesting that the cockroaches displayed a rebound effect and the woodlice did not.

The inherent differences in the biology and life history of species are a very important consideration for the differences seen in their reactions to restricted space. Chimpanzees have the longest life span of about 59 years (Herndon *et al.*, 1999), followed by woodlice (3 years; Johnson, 1982) and striped mice (1-2 years; Schradin and Pillay 2005a) and cockroaches have the shortest life span (250 days; Nojima *et al.*, 1999). The lifespan of the woodlice, striped mice and chimpanzees are much longer compared to the lifespan of cockroaches, which do not survive beyond 8 months.

The lifespan of an animal is linked to its life history strategy with different life history strategies requiring different behavioural capabilities (Mizunami *et al.*, 1999). Animals that are small with a short life span, in this case the cockroach, and have a low chance of survival into adulthood cannot invest energy in complex memory or learning as they need to spend most of their energy on producing large numbers of offspring (Mizunami *et al.*, 1999). Conversely, memory and learning are important components of the biology of longer lived animals, in this case striped mice and chimpanzees, as longer lived animals tend to respond to environmental change by modifying individual behaviour (Mizunami *et al.*, 1999). Woodlice are exceptional in that they have longer lifespan than striped mice, but this does not take into account the metabolic rates of the species and potential seasonal diapauses in woodlice (Mocquard *et al.*, 1989), which may extend the life span of these crustaceans.

Welfare and conservation implications

Since there is a strong case for the role of learned helplessness in influencing the use of restricted space across a variety of taxa, there needs to be considerations of how learned helplessness, in terms of space use, relates to animal welfare and the possible implications of animal reintroductions into natural environments.

In captive environments, if restricted space use is as a consequence of habit formation, it may be altered by providing enrichment that requires animals to utilise more space and ultimately “break the boundaries”. This can be achieved by rotating various stimuli and resources within the enclosure, like food and toys, which may encourage the animals to use the area more extensively and break the habit of staying spatially restricted. However, if restricted space use is the result of learned helplessness resulting from brain dysfunction, ideally animals should not be in captive environments. However, this is not always a realistic consideration. Therefore, there needs to be a focus on promoting increased space use and increasing controllability within the captive environment. Since learned helplessness is not dependent on contextual conditions (Mark, 1983), if animals were provided with a variety of controllable obstacles, would this promote the perception of control over a variety of situations and thus decrease the negative effects associated with learned helplessness (e.g. inactivity, hormone changes)? Would providing stimuli in blocks that mirror the old enclosure size encourage captive animals to utilise more space while maintaining spatial restrictions?

The reintroduction of animals is often difficult, particularly with chimpanzees (Goossens *et al.*, 2005) as they respond aggressively to strangers (Goodall, 1986). Reintroductions and are not always a successful process (Treves and Naughton-Treves, 1997), with the success of release programs possibly being further hindered by animals that may not use available space optimally, either by restricting their individual movements or their social spacing to the size of their original captive housing.

Personality and sex effects are also an important consideration for animal welfare as sex and personality may have an influence on how animals react to more space, whether they are released back into natural environments or given more space in captivity.

Conclusion and future studies

The previous experience of an individual or of a group of individuals in restricted space does appear to influence subsequent use of space in an enlarged area. Learned helplessness was the most likely contributor to restricted space use but restricted space use, as a result of learned helplessness, does not seem to be neuronal complexity dependent as it was seen in 3 species with varying degrees of neuronal complexity. Nonetheless, my study does not fully exclude the possibility of habit formation.

The environments of the striped mice, woodlice and cockroaches were comparatively better controlled compared to the environment of the chimpanzees; future studies on the effect of previous experiences on space use in captive chimpanzees could consider manipulating shade, temperature and spatial heterogeneity. Spatial heterogeneity is important for chimpanzees as they generally avoid open space, preferring to be close to mesh walls, corners and doorways (Ross *et al.*, 2009), and they prefer spaces above the ground (Ross and Lukas, 2006). By manipulating the various elements that the chimpanzees are exposed to (temperature, spatial heterogeneity, shade availability), it may possible to provide more definite conclusions about the effects of learned helplessness because one could identify which particular element/s influence space use in captive chimpanzees.

Given that learned helplessness does not seem to be neuronal complexity dependent, the implications of exposure to restricted space needs to be considered for all species in captive environments, especially animals in release programs. Future studies should look at the exposure time to restricted environments to evaluate how long an animal needs to be exposed to spatially restricted environments in order to develop learned helplessness. The holding time for each species could be manipulated to quantify the maximum time that an animal needs to be exposed to restricted space before developing learned helplessness. Future studies could also look at the space use of animals from release programs to assess whether these animals in unrestricted natural environments are restricting their movements and space use to the size of their original, captive housing post release. Some data collected on post-released vervet monkeys, *Cercopithecus aethiops*, showed that a troop released into suitable habitat, displayed spatial restriction several months after release (Bratt, 2010). This study indicates that spatial restriction may influence release programmes. There should also be comparisons made between individuals of different birth origin, i.e. wild caught and captive born, exposed to restricted space to assess whether animals from natural environments would be similarly affected as captive born individuals, since the behaviour and reactions of captive born animals are known to differ from wild caught counterparts (Jones *et al.*, 2011).

Finally, in order to properly distinguish between learned helplessness and habit formation, future studies should consider looking at the underlying hormonal basis of the behaviour that follows exposure to restricted space.

References

Abramson, L. Y., Garber, J. and Seligman, M. E. P. 1980. Learned helplessness in humans: An attributional analysis. pp. 3-34. *In* J. Garber and M. E. P. Seligman (Eds.), Human helplessness: Theory and application. Academic Press, New York.

Abramson, L. Y., Metalsky, G. I. and Alloy, L. B. 1989. Hopelessness depression: A theory-based subtype of depression. *Psychological Review* **96(2)**: 358-372.

Alberstadt, P. J., Steele, C. W. and Skinner, C. 1995. Cover-seeking behaviour in juvenile and adult crayfish, *Orconectes rusticus*: Effects of darkness and thigmotactic cues. *Journal of Crustacean Biology* **15(3)**: 537-541.

Allaby, M. 1999. "Idiothetic." A Dictionary of Zoology.Oxford University Press, New York.

Alonso, S. J., Castellano, M. A. Afonso, D. and Rodriguez, M. 1991. Sex differences in behavioural despair: Relationships between behavioural despair and open field activity. *Physiology and Behaviour* **49**: 69-72.

Ame, J. M., Halloy, J., Rivault, C., Detrain, C. and Deneubourg, J. L. 2006. Collegial decision making based on social amplification leads to optimal group formation. *PNAS* **103(15)**: 5835-5840.

Arakawa, H. 2005. Age dependent effects of space limitation and social tension on open-field behaviour in male rats. *Physiology and Behaviour* **84**: 429–436.

Bailey, C. H., Bartsch, D. and Kandel, E. R. 1996. Toward a molecular definition of long-term memory storage. *PNAS* **93**: 13445-13452.

Barber, J. G. 1986. The promise and the pitfalls of learned helplessness theory for social work practice. *British Journal of Social Work* **16(5)**: 557-570.

Basil, J. and Sandeman, D. 2000. Crayfish (*Cherax destructor*) use tactile cues to detect and learn topographical changes in their environment. *Ethology* **106**: 247-259.

Bates, L. and Byrne, R. 2009. Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*): Foraging and border checking. *Behavioral Ecology and Sociobiology* **64**: 247-255.

Baum, A., Fleming, R. and Reddy, D. M. 1986. Unemployment stress: Loss of control, reactance and learned helplessness. *Social Science and Medicine* **22(5)**: 509-516.

Bayley, M. Baatrup, E. and Bjerregaard, P. 1997. Woodlouse locomotor behaviour in the assessment of clean and contaminated field sites. *Environmental Toxicology and Chemistry* **16 (11)**: 2309–2314.

Beale, I. L. and Webster, D. M. 1971. The relevance of leg-movement cues to turn alternation in woodlice (*Porcellio scaber*). *Animal Behaviour* **19**: 353-356.

Beasor, T. 2006. Great negotiators: How the most successful negotiators think and behave. Gower Publishing Ltd, Hampshire.

Beattie, V. E., Walker, N. and Sneddon, I. A. 1996. An investigation of the effect of environmental enrichment and space allowance on the behaviour and production of growing pigs. *Applied Animal Behaviour Science* **48:** 151-158.

Becker, J. T., Walker, J. A. and Olton, D. S. 1980. Neuroanatomical bases of spatial memory. *Brain Research* **200**: 307-320.

Benhamou, S., Sauve, J. P. and Bovet, P. 1990. Spatial memory in large scale movements: Efficiency and limitations of the egocentric coding process. *Journal of Theoretical Biology* **145**:1-12.

Bettinger, T., Wallis, J. and Carter, T. 2005. Spatial selection in captive adult female chimpanzees. *Zoo Biology* **13(2)**: 167-176.

Boesch, C. 1991. Teaching among wild chimpanzees. *Animal Behaviour* **41**: 530-532.

Bratt, E. 2010. Behaviour and space use changes by a group of rehabilitated vervet monkeys post-release. BSc (Hons) report. University of the Witwatersrand, Johannesburg.

Bret, B. L. and Ross, M. H. 1985. A laboratory study of German cockroach dispersal (Dictyoptera: Blattelidae). *Proceedings of the Entomological Society of Washington* **87**:448-455.

Brucato, F. H., Levin, E. D., Mott, D. D., Lewis, D. V., Wilson, W. A and Swartzwelder, H. S. 1996. Hippocampal long-term potentiation and spatial learning in the rat: Effects of GABAB receptor blockade. *Neuroscience* **74**: 331–33.

Bullock, T. H. 2002. Grades in neural complexity: How large is the span? *Integrative and Comparative Biology* **42**:757-761.

Busse, C. D. 1978. Do chimpanzees hunt cooperatively? *The American Naturalist* **112 (986)**: 767-770.

Byrne, R. W. and Whiten, A. 1992. Cognitive evolution in primates: Evidence from tactical deception. *Man, New Series* **27(3)**: 609-627.

Caldarone, B. J., George, T. P., Zachariou, V and Picciotto, M. R.2000. Gender differences in learned helplessness behaviour are influenced by genetic background. *Pharmacology Biochemistry and Behaviour* **66(4)**: 811–817.

Camhi, J.M. and Johnson, E. N. 1999. High-frequency steering manoeuvres mediated by tactile cues: Antennal wall-following in the cockroach. *The Journal of Experimental Biology* **202**: 631–643.

Carpenter, F. L. 1987. Food abundance and territoriality: To defend or not to defend? *American Zoologist* **27**: 387-399

Caws, C. and Aureli, F. 2003. Chimpanzees cope with temporary reduction of escape opportunities. *International Journal of Primatology* **24(5)**: 1077-1091.

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

Chapman, C. A., Wrangham, R. W. and Chapman, L. J. 1995. Ecological constraints on group size: An analysis of spider monkey and chimpanzees subgroups. *Behaviour Ecology and Sociobiology* **36**:59-70.

Checkly, S. 1996. The neuroendocrinology of depression and chronic stress. *British Medical Bulletin* **52(3)**: 597-617.

Chourbaji, S., Zacher, C., Sanchi-Segura, C., Spanagel, R. and Gass, P. 2005. Social and structural housing conditions influence the development of a depressive-like phenotype in the learned helplessness paradigm in male mice. *Behavioural Brain Research* **164(1)**: 100-106.

Clarke, A. S., Juno, C. J. and Maple, T. L. 1982. Behavioural effects of a change in the physical environment: A pilot study of captive chimpanzees. *Zoo Biology* **1**: 371-380.

Cloarec, A. and Rivault, C. 1991. Age-related changes in foraging in the German cockroach (Dictyoptera: Blattellidae). *Journal of Insect Behaviour* **4(5)**: 661-673.

Cloudsley-Thompson, J. L. 1956. Studies in diurnal rhythms: VII. Humidity responses and nocturnal activity in woodlice (Isopoda). *Journal of Experimental Biology* **33(3)**: 576-582.

Clubb, R. and Mason, G. 2003. Captivity effects on wide ranging carnivores. *Nature* **425**: 473-474.

Coelho, A. M. Jr. and Bramblett, C. A. 1981. Sexual dimorphism in the activity of olive baboons (*Papio cynocephalus anubis*) housed in monosexual groups. *Archives of Sexual Behaviour* **10(1)**: 79-91.

Collett, T. S., Cartwright, B. A. and Smith, B. A. 1986. Landmark learning and visuo-spatial memories in gerbils. *Journal of Comparative Physiology* **158**: 835-851.

Collett, T.S. 1996. Insect navigation en route to the goal: Multiple strategies for the use of landmarks. *The Journal of Experimental Biology* **199**: 227–235.

Cooper, L. D. and Randall, J. A. 2007. Seasonal changes in home ranges of the giant kangaroo rat (*Dipodomys ingens*): A study of flexible social structure. *Journal of Mammalogy* **88(4)**: 1000-1008.

Cornwell, P. B. 1968. The Cockroach Volume 1. Hutchinson and co. (publishers) LTD. P.B. Cornwell.

Daw, N. W. and Wyatt, H. J. 1976. Kittens reared in a unidirectional environment: Evidence for a critical period. *Journal of Physiology* **257**: 155-170.

de Belle, J. S. and Heisenberg, M. 1994. Associative odour learning in *Drosophila* abolished by chemical ablation of mushroom bodies. *Science, New Series* **263(5147)**: 692-695.

De Vries H., Netto W. J., and Hanegraaf, P. L. H. 1993. Matman: A program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour* **125**:157–75.

Deneubourg, J. L., Lioni, A. and Detrain C. 2002. Dynamics of aggregation and emergence of cooperation. *Biological Bulletin* **202(3)**: 262-267

Dixon, L., Hardiman, J. R., Cooper, J. J. 2010. The effects of spatial restriction on the behaviour of rabbits (*Oryctolagus cuniculus*). *Journal of Veterinary Behaviour: Clinical Applications and Research* **5(6)**: 302-308.

Doran, D. 1997. Influence of seasonality on activity patterns, feeding behaviour, ranging and grouping patterns in Tai chimpanzees. *International Journal of Primatology* **2(18)**:183-206.

Duman, R. S., Malberg, J., Nakagawa, S. and D'Sa, C. 2000. Neuronal plasticity and survival in mood disorders. *Biological Psychiatry* **48**: 732–9.

Duncan, L. M. 2012. Spatial and social influences on the behaviour of captive chimpanzees. Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.

Duncan, I. J. H. & Petherick, J. C.1991. The implications of cognitive processes for animal welfare. *Journal of Animal Science* **69**:5017-5022.

Durier, V. And Rivault, C. 2000. Learning and foraging efficiency in German cockroaches, *Blattella germanica* (L.) (Insecta: Dictyoptera). *Animal Cognition* **3**:139-145.

Durier, V. and Rivault, C. 2001. Effects of spatial knowledge and feeding experience on foraging choices in German cockroaches. *Animal Behaviour* **62**: 681-688.

Dwivedi, Y., Mondal, A. C., Payappagoudar, G. V. and Rizavi, H. S. 2005. Differential regulation of serotonin (5HT) 2A receptor mRNA and protein levels after single and repeated stress in rat brain: Role in learned helplessness behaviour. *Neuropharmacology* **48**: 204-214.

Edney, E. B. 1968. Transition from water to land in isopod crustaceans. *American Zoologist* **8(3)**: 309-326

Edwards, E. King, J. A. and Fray, J. 2000. Hypertension and insulin resistant models have divergent propensities to learned helpless behaviour in rodents. *American Journal of Hypertension* **13(6)**: 659-665.

Eisenberg, J. F., 1976. Communication mechanisms and social integration in the black spider monkey, *Ateles fusciceps* and related species. *Smithsonian Contribution to Zoology* **113**: 2-49.

Eisenstein, E. M. and Carlson, A. D. 1997. A comparative approach to the behaviour called ‘learned helplessness’. *Behavioural Brain Research* **86**: 149-160.

Evans, H. E. 1984. Insect Biology: A textbook of entomology. Addison-Wesley Publishing Company, Massachusetts.

Fincham, F. D. and Cain, K. M. 1986. Learned helplessness in humans: A developmental analysis. *Developmental Review* **6**: 301-333.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N. and Skalski, G. T. 2001. Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *The American Naturalist* **158(2)**: 124-135.

Gold, P. E. and van Buskirk, R. B. 1975. Facilitation of the time-dependent memory processes with post-trial epinephrine injections. *Behavioural Ecology* **13**:145-153.

Goldman-Rakic, P. S. 1996. Memory: Recording experience in cells and circuits: Diversity in memory research. *PNAS* **93**: 13435-13437.

Goodall, J. 1986. Chimpanzees of Gombe: Patterns of behaviour. Harvard University Press, Massachusetts.

Goossens, B., Setchell, J. M., Tchidongo, E., Dilambaka, E., Vidal, C., Ancrenaz, M. and Jamart, A. 2005. Survival: Interactions with conspecifics and reproduction in 37 chimpanzees released into the wild. *Biological Conservation* **123**: 461–475.

GraphPad Software. (2003). GraphPad InStat, version 3.00 for Windows 95. San Diego, California, www.graphpad.com.

Greenwood, B. N., Foley, T. E., Day, H. E. W., Campisis, J., Hammack, S. H. Campeau, S., Maier, S. F. and Fleshner, M. 2003. Freewheel running prevents learned helplessness/behavioural depression: Role of dorsal raphe serotonergic neurons. *The Journal of Neuroscience* **23(7)**: 2889 –2898.

Grimes, L. 1981. Learned helplessness and attribution theory: Redefining children's learning problems. *Learning Disability Quarterly* **4(1)**: 91-100.

Hare, B. and Tomasello, M. 2004. Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour* **68**: 571-58.

Hassall, M., Edwards, D. P., Carmental, R., Derhé, M. A. and Moss, A. 2010. Predicting the effect of climate change on aggregation behaviour in four species of terrestrial isopods. *Behaviour* **147**: 151-164

Hassall, M., Tuck, J. M. and James, R. 2005. Effects of density and spatial heterogeneity on foraging behaviour and fitness correlates of *Armadillidium vulgare* (Isopoda Oniscidea). *Ethology Ecology and Evolution* **17**: 233-247

Heisenberg, M. 1998. What do the mushroom bodies do for the insect brain? An introduction. *Learning and Memory* **5**:1-10

Hellhammer, D. H., Rea, M. A., Bell, M. Belkien, L. and Ludwig, M. 1984. Learned helplessness: Effects on brain monoamines and the pituitary-gonadal axis. *Pharmacology, Biochemistry and Behaviour* **21(4)**:481-5.

Hennessy, M. B., Kaiser, S. and Sachser, N. 2009. Social buffering of the stress response: Diversity, mechanisms and functions. *Frontiers in Neuroendocrinology* **30**: 470–482.

Herbinger, I., Boesch, C and Rothe, H. 2001. Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire. *International Journal of Primatology* **22(2)**: 143-167.

Herndon, J. G., Tigges, J., Anderson, D. C., Klumpp, S. A. and McClure, H. M. 1999. Brain weight throughout the lifespan of the chimpanzee. *Journal of Comparative Neurology* **409**: 567-572.

Hoffmann, G. 1983. The random elements in the systematic search behaviour of the desert isopod *Hemilepistus reaumuri*. *Behavioral Ecology and Sociobiology* **13(2)**: 81-92

Holland, R. W., Aarts, H. and Langendam, D. 2006. Breaking and creating habits on the working floor: A Weld-experiment on the power of implementation intentions. *Journal of Experimental Social Psychology* **42**: 776–783.

Horne, J. S., Garton, E. O. and Rachlow, J. L. 2008. A synoptic model of animal space use: Simultaneous estimation of home range, habitat selection, and inter/intra-specific relationships. *Ecological modelling* **214**: 338-348

Hosey, G. R. 2005. How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science* **90**: 107–129.

Hughes, R. N. 1987. Mechanisms for turn alternation in four invertebrate species. *Behavioural Processes* **14**: 89-103.

Hughes, R. N. 1992. Effects of substrate brightness differences on isopod (*Porcellio scaber*) turning and turn alternation. *Behavioural Processes* **27**: 95-100.

Jeanson, R., Blanco, S. Fournier, R., and Deneubourg, J. L. 2003. A model of animal movements in a bounded space. *Journal of Theoretical Biology* **225**: 443-451.

Jensen, S. P., Gray, S. J. and Hurst, J. L. 2003. How does habitat structure affect activity and use of space among house mice? *Animal Behaviour* **66**: 239-250.

Johnson, C. 1982. Multiple Insemination and Sperm Storage in the Isopod, *Venezillo evergladensis* Schultz, 1963. *Crustaceana* **42(3)**: 225-232.

Johnson, V. R. Jr. 1977. Individual recognition in the banded shrimp *Stenopus hispidus* (Olivier). *Animal Behaviour* **25**: 418-428.

Jones, B. R. 2002. Role of comparative psychology in the development of effective environmental enrichment strategies to improve poultry welfare. *International Journal of Comparative Psychology* **15**: 77-106.

Jones, M. A., Mason, G. J. and Pillay, N. 2011. Correlates of birth origin effects on the development of stereotypic behaviour in striped mice, *Rhabdomys*. *Animal Behaviour* **82(1)**: 149-159.

Joshi, S. G. 2009.The interaction between stereotypy, personality and environmental enrichment in the African Striped Mouse. Unpublished MSc dissertation, University of the Witwatersrand, Johannesburg.

Kandel, E. and Abel, T. 1995. Neuropeptides, adenylyl cyclise, and memory storage. *Science, New Series* **268(5212)**: 825-826.

Kandel, E. R. 2001. The molecular biology of memory storage: A dialog between genes and synapses. *Bioscience Reports* **21(5)**: 565-611.

Keeling, L. and Duncan, I. J. H. 1989. Inter-individual distances and orientation in laying hens housed in groups of three in two different-sized enclosures. *Applied Animal Behaviour Science* **24**: 325-342.

Keeling, L. and Duncan, I. J. H. 1991. Social spacing in domestic fowl under semi-natural conditions: The effect of behavioural activity and activity transitions. *Applied Animal Behaviour Science* **32**: 205-217.

Kennett, G. A., Chaouloff, F., Marcou, M. and Curzon, G. 1986. Female rats are more vulnerable than males in an animal model of depression: The possible role of serotonin. *Brain Research* **382**: 416-421.

Kim, J. J., Song, E. Y. and Korsten, T. A. 2006. Stress effects in the hippocampus: Synaptic plasticity and memory. *Stress* **9(1)**:1-11.

Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G. and Pineda, J. 2002. Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science supplement* **70(1)**: 309-340.

Kinnaird, M. F. 1992. Variable resource defence by the Tana River crested mangabey. *Behavioural ecology and socio-biology* **31**:115-122

Kosheleff, V. P. and Anderson, C. N. K. 2009. Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. *American Journal of Physical Anthropology* **1**: 1-10.

Krashes, M., Keene, A. C., Leung, B., Armstrong, J. D. and Waddell, S. 2007. Sequential use of mushroom body neuron subsets during *Drosophila* odor memory processing. *Neuron* **53(1)**: 103-115

Krebs, J. R. and Inman, A. J. 1992. Learning and foraging: Individuals, groups and populations. *The American Naturalist, Supplement: Behavioral Mechanisms in Evolutionary Ecology* **140**: S63-S84.

Kupferman, B. 1966. Turn alternations of the pill bug (*Armadillidium vulgare*). *Animal Behaviour* **14**: 68-72.

Lehmann, J. Korstjens, A. H. and Dunbar, R. I. M. 2007. Group size, grooming and social cohesion in primates. *Animal Behaviour* **74**: 1617-1629.

Leone, E. H., Christman, M. C., Douglas, L. and Estevez, I. 2010. Separating the impact of group size, density, and enclosure size on broiler movement and space use at a decreasing perimeter to area ratio. *Behavioural Processes* **83**: 16–22.

Loesel, R. 2005. The arthropod brain: Retracing six hundred million years of evolution. *Arthropod Structure and Development* **34**: 207–209.

Lwanga J. S. 2006. Spatial distribution of primates in a mosaic of colonizing and old growth forest at Ngogo, Kibale National Park, Uganda. *Primates* **47**: 230-238.

Mackay, M. K. 2011. The behaviour of two sub-species of the striped mouse *Rhabdomys*: The role of phylogeny and the environment. Unpublished Msc dissertation, University of the Witwatersrand, Johannesburg.

Maclaurin, J. 1998. How to defeat complexity. *Australasian Journal of Philosophy* **76(3)**: 491-501.

Madison, D. M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioural Ecology and Sociobiology* **7(1)**: 65-71.

Maier, S. F. 1980. Learned helplessness and the schedule –shift hypotheses. *Journal of Research in Personality* **14**: 170-186.

Maier, S. F. and Seligman, M. E. P. 1976. Learned Helplessness: Theory and evidence. *Journal of experimental psychology: General* **105(1)**: 3-46.

Maier, S. F. and Watkins, L. R. 2005. Stressor controllability and learned helplessness: The roles of the dorsal raphe nucleus, serotonin, and corticotropin-releasing factor. *Neuroscience and Biobehavioural Reviews* **29**: 829–841.

Mark, S. F. 1983. To succeed or not to succeed: A critical review of issues in learned helplessness. *Contemporary Educational Psychology* **8**:1-19.

Marriott, B. M. and Meyers, D. M. 2005. Effects of altered enclosure size and substrates on squirrel monkey (*Saimiri sciureus sciureus*) behaviour. *American Association for Laboratory Animal Science* **44(6)**: 15-20.

Martinko, M. J. and Gardner W. L.1982. Learned helplessness: An alternative explanation for performance deficits. *The Academy of Management Review* **7(2)**: 195-204.

Matsumoto-Oda, A., Hosaka, K., Huffman, M. A. and Kawanaka, K. 1998. Factors affecting party size in chimpanzees of the Mahale Mountains. *International Journal of Primatology* **19(6)**: 999-1011.

Matthiopoulos, J. 2003. The use of space by animals as a function of accessibility and preference. *Ecological Modelling* **159**: 239-268.

McBride, G.1984. Feral animal studies in animal science: The uses and limitations of feral animal studies to contemporary animal science. *Journal of Animal Science* **58(2)**: 474-481.

McGaugh, J. L. 2000. Memory: A century of consolidation. *Science* **287(5451)**: 248-250

McGrew, W. C. and Tutin, C. E. G. 1978. Evidence for a social custom in wild chimpanzees? *Man, New Series* **13(2)**: 234-251.

Meehan, C. L. and Mench, J. A. 2007. The challenge of challenge: Can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science* **102**: 246–261.

Menzel, R. and Müller, U. 1996. Learning and memory in honeybees: From behaviour to neural substrates. *Annual Review of Neuroscience* **19**: 379-404.

Mitlohner, F. M., Galyean, M. L. and McGlone, J. J. 2002. Shade effects on performance, carcass traits, physiology, and behaviour of heat-stressed feedlot heifers. *Journal of Animal Science* **80(8)**: 2043-2050.

Mizunami, M., Weibrecht, J. M. and Strausfeld, N. J. 1998. Mushroom bodies of the cockroach: Their participation in place memory. *The Journal of Comparative Neurology* **402**: 520-537

Mizunami, M., Yokohari, F. and Takahata, M. 1999. Exploration into the adaptive design of the arthropod “Microbrain”. *Zoological Science* **16**: 703- 709.

Mizunami, M., Yokohari, F. and Takahata, M. 2004. Further exploration into the adaptive design of the arthropod “microbrain”: Sensory and memory-processing systems. *Zoological Science* **21(12)**:1141-1151.

Mocquard, J. P., Juchault, P. and Souty-Grosset, C. 1989. The role of environmental factors (temperature and photoperiod) in the reproduction of the terrestrial isopod *Armadillidium vulgare* (Latreille, 1804). *Monitore Zoologico Italiano Monografia* **4**: 455–475.

Morgan, K. N. and Tromborg, C. T. 2007. Sources of stress in captivity. *Applied Animal Behaviour Science* **102**: 262–302.

Morris, M. C. 1999. Using woodlice (Isopoda, Oniscoidea) to demonstrate orientation behaviour. *Journal of Biological Education* **33(4)**: 215-216.

Moriyama, T. 2004. Problem solving and autonomous behavior in pill bugs (*Armadillidium vulgare*). *Ecological Psychology* **16 (4)**: Abstract only 287-302.

Nadel, L. And Macdonald, L. 1980. Hippocampus: Cognitive map or working memory? *Behavioural and Neural Biology* **29**: 405-409.

Newberry, R. C. and Hall, J. W. 1990. Use of pen space by broiler chickens: Effects of age and pen size. *Applied Animal Behaviour Science* **25**: 125-136.

Newberry. R, C. 1995. Environmental enrichment: Increasing the biological relevance of captive environments. *Applied Animal Behaviour Science* **44**: 229-243.

Nishida, T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates* **9**: 167-224.

Nishimura, J. I., Endo, Y. and Kimura, F. 1999. A long-term stress exposure impairs maze learning performance in rats. *Neuroscience Letters* **273**: 125-128.

Nojima, S., Sakuma, M., Nishida, R. and Kuwahara, Y. 1999. A glandular gift in the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae): The courtship feeding of a female on secretions from male tergal glands. *Journal of Insect Behaviour* **12(5)**: 627-640.

Odberg, F.O. 1987. The influence of cage size and environmental enrichment on the development of stereotypies in bank voles (*Clethrionomys glareolus*). *Behavioural Processes* **14**: 155-173.

Ohl, F. and Fuchs, E. 1999. Differential effects of chronic stress on memory processes in the tree shrew. *Cognitive Brain Research* **7:** 379–387.

Oitzl, M. S. and de Kloet, E. R. 1992. Selective corticosteroid antagonists modulate specific aspects of spatial orientation learning. *Behavioral Neuroscience* **106(1)**: 62-71

Olton, D. S. and Papas, B. C. 1979. Spatial memory and hippocampal function. *Neuropsychologia* **17**:669-682.

Overmier, J. B. 2002. On learned helplessness. *Integrative Physiological and Behavioural Science* **37(1)**: 4-8.

Overmier, J. B. and Seligman, M. E. 1967. Effects of inescapable shock upon subsequent escape and avoidance responding. *Journal of Comparative and Physiological Psychology* **63:** 28-33.

Palagi, E. 2006. Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): Implications for natural social systems and inter-individual relationships. *American Journal of Physical Anthropology* **129**: 418-426.

Palagi, E., Cordoni, G. and Borgognini-Tarli, S. M. 2004. Immediate and delayed benefits of play behaviour: New evidence from chimpanzees (*Pan troglodytes*). *Ethology* **110**: 949-962.

Palanza, P. 2001. Animal models of anxiety and depression: How are females different? *Neuroscience and Biobehavioural Reviews* **25**: 219-233.

Park, C. R., Campbell, A. M. and Diamond, D. M. 2001. Chronic psychosocial stress impairs learning and memory and increases sensitivity to yohimbine in adult rats. *Biological psychiatry* **50(12)**: 994-1004.

Perkins, L. A. 1992. Variables that influence the activity of captive orangutans. *Zoo Biology* **11**: 177–186.

Perrin, M. R., Ercoli, C., and Dempster, E. R. 2001. The role of agonistic behaviour in the population of two syntopic African grassland rodents, the striped mouse *Rhabdomys pumilio* (Sparrman, 1784) and the multi-mammate mouse *Mastomys natalensis* (A. Smith 1834) (Mammalia Rodentia). *Tropical Zoology* **14**: 7–29.

Petty, F., Kramer, G. L. and Jordan, S. 1994. A neuronal model for learned helplessness in the rat. *Biological Psychiatry* **35**: 615-747. Abstract only: 705-706.

Powell, R., Dolan, R. And Wessely, S. 1990. Attributions and self-esteem in depression and chronic fatigue syndromes. *Journal of Psychosomatic Research* **34(6**):665-673.

Price, E. O. 1999. Behavioural development in animals undergoing domestication. *Applied Animal Behaviour Science* **65**: 245-271.

Pusey, A. E. 1990. Behavioural changes at adolescence in chimpanzees. *Behaviour* **115(3/4)**: 203-246.

Reynolds, V. 2005. The chimpanzees of the Budongo forest: Ecology, behaviour and conservation. Oxford University Press, Oxford.

Rivault, C. 1989. Spatial distribution of the cockroach, *Blattella germanica*, in a swimming-bath facility. *Entomologia Experimentalis et Applicata* **53**: 247-255.

Rivault, C. and Durier, V. 2004. Homing in German cockroaches, *Blattella germanica* (L.) (Insecta: Dictyoptera): Multi-channelled orientation cues. *Ethology* **110**: 761-777

Rodel, H. G., Monclus, R. and von Holst, D. 2006. Behavioural styles in European rabbits: Social interactions and responses to experimental stressors. *Physiology and Behaviour* **89**:180-188

Ross, S. R. and Lukas, K. E. 2006. Use of space in a non-naturalistic environment by chimpanzees (*Pan troglodytes*) and lowland gorillas (*Gorilla gorilla gorilla*). *Applied Animal Behaviour Science* **96**: 143-152.

Ross, S. R. Schapiro, S. J., Hau, J. and Lukas, K. E. 2009. Space use as an indicator of enclosure appropriateness: A novel measure of captive animal welfare. *Applied Animal Behaviour Science* **121**: 42–50.

Samuel, M. D., Pierce, J. and Garton, E. O. 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology* **54(3)**: 711-719.

Sandeman, R. E., Watson, A. H. D. and Sandeman, D. C. 1995. Ultrastructure of the synaptic terminals of the dorsal giant serotonin-IR neuron and deutocerebral commissure interneurons in the accessory and olfactory lobes of the crayfish. *The Journal of Comparative Neurology* **361**: 617-632.

Sandi, C., Loscertales, M. and Guaza, C. 1997. Experience-dependent facilitating effect of corticosterone on spatial memory formation in the water maze. *European Journal of Neuroscience* **9**: 637-442.

Santrock, J. W. 2002. Psychology (Seventh Edition). McGraw-Hill co. Inc., Texas.

Schapiro, S. J. and Bloomsmith, M. A. 1994.Behavioural effects of enrichment on pair-housed juvenile rhesus monkeys. *American Journal of Primatology* **32(3)**:159-170.

Schenk, F. and Morris, R. G. M 1985. Dissociation between components of spatial memory in rats after recovery from the effects of retrohippocampal lesions. *Experimental Brain Research* **58**: 11-28.

Schradin, C. 2006. Whole-day follows of striped mice (*Rhabdomys pumilio*), a diurnal murid rodent. *Journal of Ethology* **24**:37-43

Schradin, C. and Pillay, N. 2004a. Prolactin levels in paternal striped mouse (*Rhabdomys pumilio*) fathers. *Physiology and Behaviour* **81**: 3– 50

Schradin, C. and Pillay, N. 2004b. The striped mouse (*Rhabdomys pumilio*) from the Succulent Karoo, South Africa: A territorial group-living solitary forager with communal breeding and helpers at the nest. *Journal of Comparative Psychology* **118**: 37-47.

Schradin, C. and Pillay, N. 2005a. Demography of the striped mouse (*Rhabdomys pumilio*) in the succulent karoo. *Mammalian Biology* **70**: 84-92.

Schradin, C. and Pillay, N. 2005b. Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy* **86**: 99-107.

Sherman, A. D., Sacquitne, J. L. and Petty, F. 1982. Specificity of the learned helplessness model of depression. *Pharmacology, Biochemistry and Behaviour* **16**: 449-454.

Sherwin, C. M. and Nicol, C. J. 1997. Behavioural demand functions of caged laboratory mice for additional space. *Animal Behaviour* **53**: 67-74.

Shors, T. J. and Leuner, B. 2003. Estrogen-mediated effects on depression and memory formation in females. *Journal of Affective Disorders* **74**: 85–96.

Skinner, J. D. and Chimimba, C. T. (2005). The mammals of the southern African subregion. (Third Edition). Cambridge University Press, Cape Town

Solomon, E. P., Berg, L. R., Martin, D. W. and Villee, C. 1996. Biology (Fourth Edition). Saunders College Publishing, Fort Worth.

Song, L., Che, W., Min-Wei, W., Murakami, Y. and Matsumoto, K. 2006. Impairment of the spatial learning and memory induced by learned helplessness and chronic mild stress. *Pharmacology, Biochemistry and Behaviour* **83**: 186–193.

Sporns, O. 2003. Network analysis, complexity and brain function. *Wiley Periodicals, Inc.* **8(1):** 56-60.

Squire, L. R. 1987. Memory and Brain. Oxford University Press, New York.

StatSoft, Inc. 2001. STATISTICA (data analysis software system), version 6. www.statsoft.com.

Steenbergen, H. L., Farabollini, F., Heinsbroek, R.P. and Van de Poll, N.E. 1991. Sex-dependent effects of aversive stimulation on holeboard and elevated plus-maze behaviour. *Behavioural Brain Science* **43**:159-165.

Steenbergen, H. L., Heinsbroek, R. P. W., Van Hest, A. and Van de Poll, N. E. 1990. Sex-dependent effects of inescapable shock administration on shuttlebox-escape performance and elevated plus-maze behaviour. *Physiology and Behaviour* **48(4)**: 571-576.

Stoinski, T. S., Hoff, M. P. and. Maple T. L. 2001. Habitat use and structural preferences of captive western lowland gorillas (*Gorilla gorilla gorilla*): Effects of environmental and social variables. *International Journal of Primatology* **22(3)**: 431-447.

Strausfeld, N. J. 1998. Crustacean-insect relationship: The use of brain characters to derive phylogeny amongst segmented invertebrates. *Brain, Behaviour and Evolution* **52**: 186-206

Sugiyama, Y. and Koman, J. 1979. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* **20(3)**: 323-339.

Tolman, E.C. 1948. Cognitive maps in rats and men. *Psychological Review* **55**:189–208.

Tomsic, D., de Astrada, M. B. and Sztarker, J. 2003. Identification of individual neurons reflecting short- and long-term visual memory in the arthropod. *The Journal of Neuroscience* **23(24)**: 8539-8546.

Treves, A. and Naughton-Treves, L. 1997. Case study of a chimpanzee recovered from poachers and temporarily released with wild conspecifics. *Primates* **38(3)**: 315-324.

Uekermann, J., Daum, I., Peters, S., Wiebel, B., Przuntek, H. and Muller T.2003. Depressed mood and executive dysfunction in early Parkinson’s disease. *Acta Neurologica Scandinavica* **107**: 341–348.

Vannini, M. and Cannicci, S. 1995. Homing behaviour and possible cognitive maps in crustacean decapods. *Journal of Experimental Marine Biology and Ecology* **193**: 67-91.

Vedder, A. L. 1984. Movement patterns of a group of free-ranging mountain gorillas (*Gorilla gorilla beringei*) and their relation to food availability. *American Journal of Primatology* **7(2)**: 73-88.

Videan, E. N. 2006. Sleep in captive chimpanzee (*Pan troglodytes*): The effects of individual and environmental factors on sleep duration and quality. *Behavioural Brain Research* **169**: 187–192.

Vollmayr, B. and Henn, F. A. 2001. Learned helplessness in the rat: Improvements in validity and reliability. *Brain Research Protocols* **8**:1-7.

von Gunten, A., Fox, N. C., Cipolotti. L. and Ron, M. A. 2000. A volumetric study of hippocampus and amygdala in depressed patients with subjective memory problems. *Journal of Neuropsychiatry and Clinical Neuroscience* **12(4)**: 493-498

Warburg, M. R. and Rosenberg, M. 1978. Neurosecretory cells in the brain of *Porcellio obsoletus* (Isopoda: Oniscidea). *International Journal of Insect Morphology and Embryology* **7(3)**: 195-204.

Weiss, J. M., Goodman, P. A., Losito, B. G., Corrigan, S., Charry, J. M. and Bailey, W. H. 1981. Behavioural depression produced by an uncontrollable stressor: Relationship to norepinephrine, dopamine and serotonin levels in various regions of rat brain. *Brain Research Reviews* **3**: 167-205.

Williams, J. L., Baker, S. L., Gress, J. E. and Bennet, G. 1998. Effects of predator-induced stress and age on working memory in rats. *Psychological Record* **48(3)**: 355-373.

Williams, J. M., Pusey, A. E., Carlis, J. V., Farms, B. P. and Goodall, J. 2002. Female competition and male territorial behaviour influence female chimpanzees’ ranging patterns. *Animal Behaviour* **63**: 347-360.

Winkler, J., Suhr, S. T., Gage, F. H., Thal, L. J. and Fisher, L. J. 1995. Essential role of neocortical acetylcholine in spatial memory. *Nature* **375(6531)**: 484-487

Wolpe, J. 1968. Psychotherapy by reciprocal inhibition. *Integrative Psychological and Behavioural Science* **3(4)**: 234-240.

Wrangham, R. W. and Smuts, B. B. 1980. Sex differences in the behavioural ecology of the chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertilisation: Supplement* **28**: 13-31.

Yacoubi, M. E. and Vaugeois, J.M. 2007. Genetic rodent models of depression. *Current Opinion in Pharmacology* **7(1)**: 3-7.

Yamagiwa, J. 1999. Socioecological factors influencing population structure of gorillas and chimpanzees. *Primates* **40(1)**: 87-104.

Yin, H. H. and Knowlton, B. J. 2006. The role of the basal ganglia in habit formation. *Nature Reviews Neuroscience* **7**: 464-476.

Zahavi, A.1971. The social behaviour of the white wagtail *Motacilla alba alba* wintering in Isreal. *Ibis* **113(2)**: 203–211.

Zar, J.H. 1996. <u>Biostatistical analysis</u>. New Jersey: Prentice-Hall.

Zars, T. 2000. Behavioural function of the insect mushroom bodies. *Current Opinion in Neurobiology* **10(6)**: 790-795

Zhukov, D. A. and Vinogradova, K. P. 2002. Learned helplessness or learned inactivity after inescapable stress? Interpretation depends on coping styles. *Integrative Physiological & Behavioural Science* **37(1)**: 35-43.

Zimmer, M. and Topp, W. 1997. Does leaf litter quality influence population parameters of the common woodlouse, *Porcellio scaber* (Crustacea: Isopoda)? *Biology and Fertility of Soils* **24**:435–441.

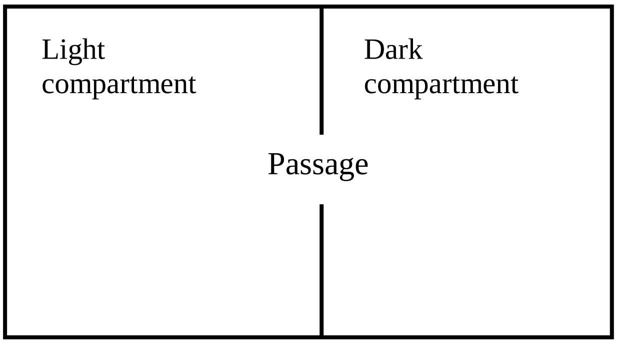
Appendix

Personality tests

Four tests were used to assess the personality type of non-stereotypic striped mice (after Joshi 2009). Bold and shy categories were allocated to individuals based on the responses to all 4 personality tests. Bolder individuals would have spent more time in the light compartment in the light-dark test; they would have had a slower startle response in the startle-response test and shown less anxiety related behaviours. Bolder individuals would recover more quickly from the startle response test and thus have a shorter latency to return to the light chamber, they would have spent less time near the periphery of the cage in the open field test, they would have had a shorter latency to approach the novel object and they would have showed higher frequencies of exploratory behaviours e.g. rearing/jumping or biting and sniffing novel objects; and lower frequencies of anxiety related behaviours e.g. freezing, digging.

Light-dark and startle response tests

For these 2 tests, I used a glass tank (400 mm x 250 mm x 120 mm), that was divided into 2 compartments by a Perspex® wall: one half of the tank was painted black (dark) and the other half was transparent (light; Appendix Figure). The wall had a small opening for the test subject to move between the light and dark compartments (Appendix Figure). A lid was placed on top of the tank to prevent the test subject from escaping while video recording took place. The tank was cleaned with disinfectant soap and air-dried between tests to reduce carry-over odour effects.



Appendix Figure**.** A diagrammatic representation of the experimental tank used to assess the personality of test subjects in light-dark and startle response tests.

Light-dark test

At the start of tests, a test subject was placed in the dark compartment. Behaviour was video recorded for 5 minutes immediately thereafter. Behaviour was only scored in the "light" side of the test tank where the subject was visible. I scored the following variables from the video recordings: latency to move from the dark to the light compartment; latency to return to the dark compartment after first entry into the light compartment; number of transitions from the light to the dark compartment; and the location (i.e. centre or periphery) of where the most time was spent in the light compartment. I also recorded the frequency of anxiety-related behaviours (e.g. freezing, jumping, cage digging, rearing) and grooming (Appendix Table) in the light compartment.

Startle response test

The startle response test followed immediately after the light-dark test. On the test subject's next entry into the light compartment (at the end of the 5 minute light-dark test), I startled the subject by clapping my hands next to the tank, and it immediately retreated into the dark area. All the parameters scored in the light-dark test were scored in this test for a further 5 minutes.

Open-field test

Each test subject was placed singly in the centre of a tank (400 mm x 250 mm x 120 mm) and behaviour was then video recorded for 10 minutes. I recorded the frequency of anxiety-related behaviours (freezing, digging, rearing, jumping; Appendix Table) and the location of the test subject (centre or periphery) in the tank.

Novel object test

The novel object test followed immediately after the open-field test. A novel round plastic object (110mm x 10mm x 15mm) was placed in the opposite corner of the tank, relative to the subject. The individual was video recorded for a further 10 minutes, and the frequencies of the following behaviours were scored: latency to approach the novel object; behaviours displayed on approaching the novel object (sniffing, biting, rearing and jumping; Appendix Table); the number of rears and jumps (indicating exploration); and the number of grooming events.

Appendix Table. Definition of behaviours scored in the open-field and light-dark tests for striped mice *Rhabdomys*

Behaviour	**Description**
Freezing	Individual freezes and crouches, usually in the corner of the tank
Jumping	Individual jumps in corners of the tank on its hind legs but not repetitively
Cage digging	Individual digs in the corners of the tank
Rearing	Individual stands on its hind legs and leans against the wall of the tank and rears against it
Grooming	Individual sits and cleans itself
Sniffing	Individual sniffs the novel object which is indicative of interaction with novel object
Biting	Individual bites and/or manipulates the novel object which is indicative of interaction with novel object