AN EXAMINATION OF SOCIAL AROUSAL AND ITS IMPLICATIONS

FOR SOCIAL COGNITION IN THE SOUTH AFRICAN VERVET

MONKEY.

PETRA L. MCDOUGALL

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Behaviour and Evolution Research Group
Department of Psychology
University of Lethbridge
Lethbridge, Alberta, Canada

Abstract

Self-directed behaviours (SDB) were recorded as a behavioural indicator of arousal in free-ranging vervet monkeys (*Chlorocebus aethiops*) inhabiting the Klein Karoo of South Africa. Measurement of SDB allowed for changes in arousal to be correlated with particular social situations, potentially providing insight into how monkeys perceive their social world. The research presented here is divided into three core chapters demonstrating that 1) arousal is influenced to a greater extent by degree of association than by hierarchical rank, 2) that an individual's level of arousal is influenced by its neighbour's spatial location, and 3) that habituated animals that no longer perceive humans as a direct threat nevertheless continue to respond to their presence in other ways. Overall, SDB appears to be a useful, non-invasive, simple means of investigating social arousal and its use has elucidated several key findings regarding the perception of social space and social partners in vervet monkeys.

Acknowledgements

Spending the past two years with the Barrett & Henzi lab has taught me a great deal about scientific research and the challenges of academia. I have witnessed truth in the popular phrase: 'the more you know, the more you know you don't know', as I realized that I could have easily consumed another two years reading literature surrounding my topic. Most of all, however, I have learned valuable lessons from wonderful debates and discussions with my supervisors, Louise Barrett and Peter Henzi, and all of the lab members. Our Friday meetings were always something to look forward to, and turned discussions of work into fun and entertaining learning experiences.

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Stress. It's what happens when your gut says 'no', but your mouth says 'sure I can!'

- Common proverb

The perfect no-stress environment is the grave.

- Greg Anderson

Chapter 1:

INTRODUCTION

1.1 Investigating social relationships in non-human animals.

As an intensely social species, humans are naturally inclined to focus their efforts on understanding social relationships. For the majority of us, the most commonly encountered species daily is fellow *Homo sapiens*; however, our folk psychological tendencies regularly extend to interpretations of relationships in non-human species, particularly among those that resemble us more closely (Eddy, Gallup Jr, & Povinelli, 1993). Anthropomorphism – the tendency to attribute human characteristics to non-human animals or objects - can indeed lead us astray in our endeavours to explain non-human social relationships; nevertheless, it has arguably been beneficial in generating research questions and stimulating debate regarding similarities in cognition between humans and other species (Burghardt, 1991). It has also been suggested, however, that scientists should avoid examining animal sociality from an anthropocentric view point; i.e., rather than investigating which human traits animals do and do not possess, research should focus on how animal relationships function in their world, and recognize that this may be very different from our own perception of the world (Barrett, Henzi, & Rendall, 2007). Failing to recognize anthropocentrism in the study of non-human social cognition places us at risk for drawing conclusions before the subject has been thoroughly explored (Barrett, et al., 2007). Understanding how an animal perceives and acts in the world is more than merely determining whether or not they possess particular human-like forms of cognition. Evolution acts to produce unique organisms best adapted to their particular

environment, thus, if we determine only whether a species possesses certain human forms of cognition, scientists may be ignorant of the most informative and interesting aspects of cognitive evolution.

In examining social relationships in non-human animals, the first thing to note is that there are two broad classes of social species in the animal kingdom: independently gregarious and socially cohesive. The first class comprises social groups such as large herds of ungulates (e.g. caribou, wildebeest), or flocks of birds (e.g. flamingos), that aggregate independently to a shared, localized source of attraction (Emlen, 1952). This source of attraction could be a feeding site, resting spot, or the presence of other individuals (Emlen, 1952). The second class of social animals are those that remain in stable, cohesive, social groups. In comparison to independent aggregations of animals, the relative permanence of these cohesive groups allows for individual recognition of group members and the development of variable individualized relationships built on past interactions (de Waal & Tyack, 2003). It is the relationships within these individualized societies that will be the topic of investigation in the following chapters.

The ability to recognize and interact with group members on an individual level necessarily means that each possible dyad may have its own unique relationship. These unique dyads increase in number exponentially as group size increases linearly, thereby creating an exceedingly large number of differing relationships within a relatively small group. For an individual living in a group with 70 members (approximately the size of the study group in the investigation to follow), a total of 2415 possible dyads exist

[(70*69)/2]. How does a single animal keep track of so many relationships?

Before addressing this question, it is essential to take note of an important difference between human and non-human animal cognition to prevent unnecessary anthropomorphizing. This difference concerns mental time travel (MTT): the ability to recall past events and imagine future scenarios. It is thought that MTT arises from the ability to use representations from physical experiences in the world, such as size or distance, to create mental representations of non-physical phenomena that cannot be acted upon or perceived with the senses (e.g., time)(Casasanto & Boroditsky, 2008). In other words, it is argued that humans use the concept of space as a metaphor to create a concept of time (Boroditsky, 2000), thereby allowing extension of the metarepresentational self into the past and future. There is currently no convincing evidence that non-human animals are capable of MTT (Suddendorf & Busby, 2003; Suddendorf & Corballis, 2007), and due to the subjective 'mental' nature of MTT it is likely to be a difficult, if not futile, avenue for scientific inquiry. Relationships in non-human animals are therefore likely to differ in that the apparent long-term qualities that define a 'relationship' in human terms (e.g. value, investment) are more likely to be emergent properties, or by-products, stemming from more immediate goal directed behaviour. In other words, although their behaviour may, in many ways, be appropriate for the maintenance of long term relationships, it is suggested that, mentally, animals may be 'stuck in time' (Roberts, 2002).

Anthropomorphically guided inquiries into the nature of non-human social relationships

have allowed scientists to create complex explanations for seemingly complex social behaviours (e.g., Machiavellian intelligence (Byrne & Whiten, 1988)), but behavioural complexity does not necessarily imply cognitive complexity (Barrett, et al., 2007). The emergent properties and apparent complexity that human observers associate with individualized relationships may not be so complex. Rather, these behavioural patterns may be guided by simple emotional mechanisms.

1.2 Could emotions be guiding social behaviour?

The term emotion has often been avoided in the study of animal behaviour as it suggests a subjective experience (Aureli & Schino, 2004). Although no single agreed upon definition of emotion exists (Kleinginna & Kleinginna, 1981), it is generally granted that emotions are internal psychological states (Cabanac, 2002), but does this mean that they are not available for scientific inquiry? The subjective 'mental' experience is only part of what defines an emotion, as there are many physiological and behavioural aspects of emotion that are overtly measurable. In fact, the term emotion derives from the Latin '*emovere*', translating to 'out movement'. This implies that emotions were initially conceived of as outward behavioural expressions of perceptual states. Bradley and Lang (2000) describe three basic components of any emotion: behaviour, feeling, and physiology. Thus, although the 'feeling' component of an emotion may be a difficult avenue for objective scientific inquiry, the behavioural and physiological components of emotions should not be overlooked. Furthermore, using emotions as a way to investigate the interaction between perception and action need not require any interpretation of the 'feeling' component. For example, rather than asking about the subjective mental

experience, investigators of emotion in the field of artificial intelligence pose very different questions, such as, "Given certain behaviours that we find interesting, what are the underlying mechanisms?" (Pfeifer, 1994). This approach allows scientists to avoid problems associated with subjective experiences and instead focus on the function of emotions.

Recent interest in the field of affective neuroscience has also reinvigorated ideas concerning the possibility of investigating emotion in non-human animals (Panksepp, 1998). The limbic system; a collection of brain structures located within the inner border of the cortex, is the primary centre of the brain associated with emotion. This system comprises a collection of structures including the cingulate gyrus, parahippocampal gyrus, amygdala, and hippocampus that function to control the expression of emotions. Preservation of the limbic system throughout evolutionary history has made cross-species similarities in basic emotions a reasonable assumption (Panksepp, 1982) and the taboo on investigations into non-human animal emotions has begun to dissipate.

For the purpose of this study, I define emotion as a physiological event accompanied by behavioural tendencies and internal psychological states that together act as an interface to mediate perception of the environment and action within it, with the goal of maintaining homeostasis. Emotions can therefore be seen as an intervening variable that allow for expedient assessment of a situation and produce flexible responses suited to the occasion (Aureli & Schaffner, 2002; Aureli & Schino, 2004). In other words, an individual's past history of interaction with a particular partner, including the frequency and quality of those interactions, are reflected in the individual's emotional response to

situations involving that partner. Emotions can therefore be viewed as a method of 'bookkeeping' of past interactions, thereby providing an expedient assessment of the present situation, and subsequently influencing the individual's response to the current social conditions (Aureli & Schaffner, 2002). For example, consider a situation in which a friend is helping you carry a heavy box and he/she stumbles and drops the box. The history of events leading up to the incident greatly influence the emotions experienced: you may show concern as to whether your friend is alright after their fall, or, if your friend has a history of being clumsy and not paying attention to where he/she is going, you may be angry with them for potential harm to yourself as a result of their clumsiness. Alternatively, if your mother has suggested that you don't attempt to move the box because its contents are heavy and very fragile, you may become worried that your mother will be angry with the two of you and you may decide not to continue with moving the box, but rather, to hide the damaged contents. These are only a few of the numerous alternative emotions that could occur as a result of differing perceptions based on a history of interactions. Furthermore, each emotional response will likely result in different subsequent actions within the world. Emotions therefore reflect a bookkeeping of past events and prompt and animal to act in manner appropriate to the current circumstances. The recent rise in research on neuroscientific, physiological, and behavioural correlates of affect (Berridge & Kringelbach, 2008; Bradley, Miccoli, Escrig, & Lang, 2008; Panksepp, 1998; Reefmann, Wechsler, & Gygax, 2009), combined with the efficient explanatory power of emotional mediation, suggest that emotion is a good candidate for providing an accurate and effective means of investigating an animal's perception of various social stimuli.

1.3 Measuring emotion

Although the internal 'mental' portion of an emotion may not be observable, there are many physiological and behavioural aspects of emotion that are overtly measurable. Studies of emotion in humans and other animals have employed methods such as: infrared thermography to detect changes in blood flow (Stewart, Webster, Schaefer, Cook, & Scott, 2005), measurement of visible sclera (Sandem, Janczak, Salte, & Braastad, 2006), frequency of ear posture changes (Reefmann, et al., 2009), patterns of cardiorespiratory activity (Aureli, Preston, & De Waal, 1999; Rainville, Bechara, Naqvi, & Damasio, 2006), and changes in rate of displacement activities such as self-directed behaviours (Maestripieri, Shino, Aureli, & Troisi, 1992; Schino, Perretta, Taglioni, Monaco, & Troisi, 1996; Troisi, 2002). The research presented here focuses on self-directed behaviours as a behavioural index of arousal changes in 11 free-ranging, female, vervet monkeys (*Chlorocebus aethiops*). According to the circumplex model of affect, arousal is one of two fundamental systems for which emotions are comprised (Russell, 1980; Posner, et al., 2005). Arousal, or alertness, is a measure of the intensity of the emotion, whereas valence is a measure of the pleasure or displeasure of the emotion (Russell, 1980; Posner, et al., 2005). In keeping with the terminology of the current literature on self-directed behaviour, the term anxiety is often used in the research that follows. It must, however, be noted that the term anxiety is used with reference only to the intensity of the emotion with no regard as to the valence (see section 1.4).

Self-directed behaviours (SDB) are displacement activities that do not appear to be related to their everyday purpose but, rather, appear to be an outlet for pent-up

motivational energy (Delius, 1967; McFarland, 1966; Spruijt, Van Hooff, & Gispen, 1992). It has been suggested that the act of engaging in a displacement activity may release endorphins that aid in reducing arousal, thereby providing a homeostatic mechanism for the maintenance of an optimal level of arousal (Spruijt, et al., 1992). In some cases, exposure to chronic stress can lead to extreme forms of displacement behaviour such as the excessive feather plucking that is frequently observed in captive parrots and domestic fowl (Owen & Lane, 2006; van Zeeland et al., 2009). Once these displacement behaviours are habitual they may become self-reinforcing and can be very difficult to eliminate. Disorders involving displacement activities are also seen in humans (e.g., trichotillomania [excessive hair pulling], and onychophagia [compulsive nail biting]), and are thought to be related to those forms that are manifest in non-human animals (Feusner, Hembacher, & Phillips, 2009). Knowledge of the role that displacement activities play in normally functioning individuals (both human and non-human) could therefore be of importance in understanding how to prevent and treat these disorders (Feusner, et al., 2009).

In normally functioning animals, self-directed behaviours have been demonstrated to be a reliable indicator of changes in arousal. Changes in rate of SDB correlate with situations of apparent stress (e.g., during and immediately following agonistic interactions) (Maestripieri, et al., 1992; Spruijt, et al., 1992; Troisi, 2002), as well as with subjective self-ratings of anxiety, guilt and disapproval in humans (Troisi, 2002). Additionally, administration of anxiety-eliciting and anxiety-reducing drugs results in a corresponding increase or decrease in rate of SDB (Schino, et al., 1996). SDB has thus been used to

investigate arousal in a variety of species and environmental conditions (e.g., fish: Clement, Parikh, Schrumpf, & Fernald, 2005; rodents: Cohen & Price, 1979; Hansen & Drake af Hagelsrum, 1984; birds: Hughes, Waluda, Stone, Ridout, & Shears, 2008; primates: Maestripieri, et al., 1992).

In the primate lineage, there has been particular interest in using measures of SDB to assist in understanding how individuals perceive their social world. Uncertainty regarding the behaviour of a social partner is thought to increase anxiety, and support for this argument comes from evidence that rates of SDB increased when unfamiliar pairs of macaques were placed together (Schino, Maestripieri, Scucchi, & Turillazzi, 1990), and that intermediate-ranking macaques exhibited a higher rate of SDB during feeding time, possibly due to uncertainty as to how they should behave (Diezinger & Anderson, 1986). Additionally, studies of post-conflict reconciliation (e.g., contact or proximity seeking in the period following aggression) are suggested to support the uncertainty hypothesis by demonstrating that SDB increases in the period following conflict, while a reduction in SDB is observed following reconciliation (Aureli & Smucny, 2000; Aureli & Van Schaik, 1991),

There are also a number of studies demonstrating the arousing effects of proximity to dominant individuals (Castles, Whiten, & Aureli, 1999; Pavani, Maestripieri, Schino, Turillazzi, & Scucchi, 1991; Troisi & Schino, 1987). Several recent studies, however, found no effect of neighbour dominance on rate of SDB (Daniel, dos Santos, & Vicente, 2008; Kutsukake, 2003; Manson & Perry, 2000), thereby calling into question the theory

that proximity to dominant individuals produces an increase in arousal due to uncertainty and an increased risk of aggression (Aureli & Schino, 2004). The role of association patterns between individuals has also been called into question, as the two studies that specifically addressed this issue produced conflicting results (Kutsukake, 2003; Manson & Perry, 2000). The goal of the research presented in this thesis is to generate a more comprehensive view of how these variables might influence arousal while accounting for the current discrepancies between studies. A third variable that takes into account the spatial location of neighbours will also be introduced, in anticipation that it will provide insight into how vervet monkeys perceive their social space.

1.4 A word on terminology

Many studies of displacement activities or SDB correlate these behaviours with changes in anxiety or stress. It is important to note, however, that an increase in anxiety or stress merely refers to an increase in emotional intensity, with no specification of whether it is due to positive or negative emotional valence. It is possible, and common, to experience positive anxiety. Think about your first time on skis or a snowboard, taking a ride on a rollercoaster, or white water rafting down rapids. Even everyday social experiences such as becoming acquainted with someone new, or going for lunch with someone, can induce positive affect (McIntyre & Watson, 1991) and heighten arousal. Many indicators of changes in emotional intensity do not distinguish between positive and negative arousal. For example, Bradley et al. (2008) found that changes in pupil diameter reflected increases in emotional arousal, but these changes did not differ depending on whether the stimuli were pleasant or unpleasant. Similarly, there is no evidence that increases in SDB

reflect only negative arousal.

Although a case for positive anxiety or stress could be made, for most readers the term anxiety will carry negative connotations. The current literature refers to increases in displacement activities as reflecting an increase in anxiety (e.g., Troisi, 2002); however, in some cases I have chosen to use the term arousal to avoid any implication that increases in SDB rate reflect an increase only in negative emotion. When the term anxiety is used, it is with the assumption that positive anxiety may also be a contributing factor. Additionally, there need not always be a distinction drawn between negative and positive arousal because, by its very nature, arousal is often representative of both. Laboratory studies of anxiety using rodents as subjects have developed a series of tests that induce an approach-avoidance conflict resulting in an increase in arousal (Blanchard, Blanchard, Griebel, & Nutt, 2008). One commonly used test is the elevated plus maze. The maze typically contains four arms (two covered and two exposed), and it is thought that the drive to explore the novel exposed area is counterbalanced by fear of open spaces and the comfort associated with sheltered areas. The maze has therefore become a popular tool for investigating aspects of personality, genes, hormones or pharmaceuticals as they relate to anxiety (Blanchard, et al., 2008). Standing on the edge of a cliff, peering down to your friends calling you from the water below, represents heightened stress/arousal due to approach-withdrawal conflict. The thrill of the jump, approval from your friends, and subsequent bragging rights, may all be pushing you in one direction, but fear of heights, and risk of injury, may be pulling you back. Life is made up of approach-withdrawal conflicts that keep us at an optimal level of arousal, and when things become

too one-sided, we often become bored and go in search of situations to heighten our arousal. For this reason, I have chosen to open my thesis with two quotes regarding stress (page x). The first quote captures the approach-withdrawal conflict perfectly, and I think it is representative of many things in life that we would consider 'fun'. The second quote reminds us that life is full of stress; therefore, if stress is such an undesirable thing, then it follows that life should be too, but this is clearly not the case. Stress is often our motivating factor to take action in life. As readers, it is therefore important to consider an optimal level of arousal as being desirable and adaptive in creating animals that are alert, attentive, and ready to act in the world.

1.5 Aims of the current thesis

My research proposes to use self-directed behaviours as an indicator of arousal in free-ranging vervet monkeys (*Chlorocebus aethiops*) to investigate several social variables that will lead to a more comprehensive understanding of how monkeys perceive their social world. The first chapter will investigate the effects of neighbour dominance rank and degree of association on changes in arousal. It is predicted that research on a wider range of species and populations will assist in explaining discrepancies in previous research. I present possible explanations for variation in previous results that are consistent with the results obtained in the current project, with hope that further research will continue to test the propositions set out here.

Additionally, my research will test the effects of a new variable – the spatial location of neighbours – on rates of SDB. Past research has focused on the mere presence of a stimulus in altering arousal; however, the effect a stimulus has on arousal may be

dependent on whether it is the current focus of attention. The ability to engage in a particular behaviour (such as interacting with a social partner) is dependent on an animal's capability to *perceive* opportunities and possibilities for action; these are termed "affordances" (Chemero, 2003; Gibson, 1979). Head and body orientation provide a good indicator as to the focus of social attention (Emery, 2000; Langton, Watt, & Bruce, 2000), and mutual attention is a basic requirement for social interaction (Kidwell & Zimmerman, 2007). It is therefore predicted that nearby social stimuli that are located behind the focal animal will not produce the same arousing effects as stimuli that are in a location where they can be easily perceived. Investigating this additional variable may help to explain some of the variation in previous results and will allow for more precise hypotheses to be made regarding sources of social arousal.

The final data chapter explores the influence of human presence on the behaviour of free-ranging vervet monkeys. Much scientific research surrounding the behaviour of wild animals, particularly in the field of primatology, is based on habituation of subjects prior to the recording of observational data (Williamson & Feistner, 2003). The term habituation originated from studies of physiology and learning to describe the reduction in response strength due to repeated exposure to stimuli that was not followed by any type of reinforcement (Thorpe, 1963). Field biologists then began using repeated non-reinforced contact with their study species to lead "ultimately to the ignoring of an observer" (Williamson & Feistner, 2003) such that data collected from 'habituated' animals was not affected by observer presence. There is an accumulating body of evidence, however, suggesting that habituated animals that no longer perceive humans as

a direct threat nevertheless continue to respond to their presence in other ways (Beausoleil, Stafford, & Mellor, 2006; Jack et al., 2008; Nishida, Matsusaka, & McGrew, 2009; Rasmussen, 1991). Although seemingly intuitive, the majority of behavioural studies conducted on 'habituated' animals fail to acknowledge to presence of the observer, despite strict precautions during the habituation process to ensure that the animals are not fearful of, or expectant for resources (e.g., food) from observers It is important to remain informed as to how observers influence the behaviour of habituated animals so that experiments and data collection protocols can be designed to minimize any observer effects. In this study, observer location was examined using the same methodology used to investigate the arousing effects of conspecifics in various spatial locations and will provide insight into how a vervet's perception of human observers changes with increasing habituation.

Chapter 2:

METHODS

2.1 General Overview of Vervet Monkey Ecology and Behaviour

The vervet monkey (*Chlorocebus aethiops*) is a semi-terrestrial catarrhine primate that - as one of the most widespread primates in Africa - inhabits nearly every country on the continent. In addition to the African continent, vervet monkeys also inhabit parts of the Caribbean, such as Barbados and St. Kitts. DNA sampling has indicated that these Caribbean populations are native to West Africa and it is thought that they arrived on the islands in the 17th and 18th centuries aboard ships involved in the slave trade from the ports of West Africa (van der Kuyl, Dekker, & Goudsmit, 1996).

Initially grouped with other guenons (*Cercopithecus*), the taxonomic classification of the vervet monkey has recently changed, placing them within the genus, *Chlorocebus* (Groves, 2001). The current consensus is that there are six species of vervet monkey in Africa (*Ch. aethiops*, *Ch. cynosuros*, *Ch. djamdjamensis*, *Ch. pygerythrus*, *Ch. sabaeus*, and *Ch. tantalus*), the southernmost species (*Ch. aethiops*) is the subject of the research presented here.

In appearance, South African vervets have a silvery gray coat (in contrast with the shades of green, olive brown, and yellow present in other *Chlorocebus* species) and the fur on their underside is white in addition to a white band of fur that extends across the forehead. The skin on their face, hands and feet is black, and the males have red penises with bright blue scrotal areas. In addition to the brightly coloured genitals possessed by males, there is also a sexual dimorphism in size, with males weighing an average of 5.5 kg and females an average of 4.1 kg (Cawthon Lang, 2006).

Vervet monkeys are diurnal, traveling between 665-2670 meters per day, and are comfortable in both terrestrial and arboreal habitats, but they sleep in trees at night to avoid predation (Harrison, 1983). Their home range size varies widely depending on habitat and resource availability, from 0.06 km^2 on St. Kitts to 1.78 km^2 in Senegal (Harrison, 1983). The presence of water and suitable sleeping trees appear to be the only limitations to their distribution (Burton, 1995).

Vervets are not only generalists in terms of habitat, but also with respect to diet. Their diet comprises every type of food known to be eaten by primates (a characteristic shared with savannah baboons (*Papio sp.*)), including leaves, gum, seeds, nuts, grasses, fungi, fruit, flowers, buds, shoots, berries, invertebrates, birds and bird eggs, lizards, rodents, and other vertebrate prey (Cawthon Lang, 2006). As expected, where resources are plentiful, population density can become high and home ranges small. Population density ranges from 9 individuals per square kilometre in areas of low resource availability to a remarkable 255 individuals per square kilometre in resource rich habitats such as agricultural areas (Harrison, 1983). This increase in density does not necessarily bring with it an increase in group size. In fact, the average group size on Barbados (an area of high density) is only 15.3 (Horrocks, 1986), which is low compared with the overall average of 25 individuals per group (Fedigan & Fedigan, 1988; Struhsaker, 1967). Vervets live in multi-male/multi-female groups in which the females remain in their natal groups for life, while males transfer to another troop upon reaching adolescence. This is known as female philopatry and results in a group of closely related adult females (and their sexually immature offspring) co-residing with slightly fewer unrelated adult males. The sex ratio in vervet troops averages 1.5 females per male and each sex has its own

linear dominance hierarchy (Cawthon Lang, 2006). Male hierarchies are often fluid, whereas female hierarchies are generally stable and governed by maternal rank inheritance (Cheney & Seyfarth, 1983; Struhsaker, 1967) - a process by which female offspring take up a position in the hierarchy directly below that of their mother. Vervet monkeys are seasonal breeders with the breeding season in South African vervets being confined to a period of approximately 2-3 months beginning in late April. During this time, females undergo ovulation with a menstrual cycle of approximately 32.5 days (Eley, Tarara, Worthman, & Else, 1989). Gestation is an average of 163-165 days (Eley, et al., 1989) and females reach sexual maturity at approximately four years of age, thereafter producing a single offspring every one to two years.

2.2 Study Site

The study site is situated in the semi-arid Klein Karoo of South Africa (32º 22`S, 24º52`E) at an altitude of 846m. With a mean annual rainfall of 330 mm, most of the surrounding area is uninhabitable by vervets apart from the woodland surrounding drainage-line riverbeds. These riverbeds only flow in times of heavy rain in their catchment area, but nonetheless contain fairly permanent pools of water throughout most of the year. The woodland surrounding the milk river, where the focal study troop resides, is dominated by acacia (*Acacia karoo*), Karee (*Rhus lancea*), and Peruvian pepper (*Schinus molle*), all of which are primary food sources. The Riverside Troop (RST) utilized only one sleeping site for the duration of the study and it included several mature Peruvian pepper trees in which the monkeys slept. The site bordered on the river bed at a location where there was a semi-permanent water source for the majority of the

study. This water source was the last known source for the three troops that bordered the area (RST, PT, and SWT) and was the site of many aggressive inter-troop encounters as water resources became scarce (McDougall, Forshaw, Barrett, & Henzi, 2010).

A second troop, River-bend Mob (RBM), with a territory located upstream (north) of RST, was also habituated and followed daily. However, data were not collected in sufficient quantity to allow for subsequent analysis and comparison with RST.

The size of the area utilized by RST was approximately 1 km long by 500 m wide. This territory had boundaries which overlapped slightly with three neighbouring troops (Figure 1). The region to the west was uninhabited by vervet monkeys and was primarily open scrub land with little vegetation. Once water resources had become depleted, RST (along with neighbouring troops) utilized this open land as a corridor for travel to a water access point further downstream (McDougall, et al., 2010) (Figure 1).

One other primate species - the chacma Baboon (*Papio ursinus*) - inhabited this region and occasionally used the same sleeping site as RST. The vervet monkeys foraged alongside the baboons when they were present, and although baboons have been known to prey upon vervet monkeys in other locations (e.g., Soutpansberg region of South Africa, personal observation), they were never observed to engage in any predatory behaviour towards the vervets in this area. One adult female and one sub-adult female disappeared during the study period. Both monkeys appeared healthy before their disappearance, and in the latter case, fur and part of a chewed skull were found at the sleeping site in the days following her disappearance, therefore predation was suspected in both instances. Neither of these females were focal animal subjects for the data presented here.

Potential predators inhabiting the area include caracal (*Caracal caracal*), cheetah (*Acinonyx jubatus*), puff adder (*Bitis arietans*), cape cobra (*Naja nivea*), black backed jackal (*Canis mesomelas*), and Cape eagle owl (*Bubo capensis*). Other mammals commonly encountered in the area during the study period include:

Oryx/Gemsbok (*Oryx gazelle*)
Common Eland (*Taurotragus oryx*)
Greater Kudu (*Tragelaphus strepsiceros*)
Red Hartebeast (*Alcelaphus buselaphus*)
Common Duiker (*Sylvicapra grimmia*)
Steenbok (*Raphicerus campestris*)
Impala (*Aepyceros melampus*)
Springbok (*Antidorcas marsupialis*)
Waterbuck (*Kobus ellipsiprymnus*)
Meerkat (*Suricata suricatta*)
Cape Porcupine (*Hystricidae africaeaustralis*)

Bushpig (*Potamochoerus larvatus*)
Plains Zebra (*Equus quagga*)
Water Buffalo (*Syncerus caffer*)
White Rhino (*Ceratotherium simum*)
Water mongoose (*Atilax paludinosus*)
Giraffe (*Giraffa camelopardalis*)
Yellow mongoose (*Cynictis penicillata*)
Spring hare (*Pedetes capensis*)
Aardvark (*Orycteropus afer*)
Dassie/Rock hyrax (*Procavia capensis*)
Scrub hare (*Lepus saxatillis*)
Bat eared fox (*Otocyon megalotis*)

Additionally, leopard tortoises (*Geochelone pardalis*) were in abundance year round, and during the summer months water monitors (*Varanus salvator*) were regularly sighted. One species of bird, the fork tailed drongo (*Dicrurus adsimilis*), regularly engaged in aggressive encounters with the vervets - diving at them from above, (with occasional contact) and vocalizing.
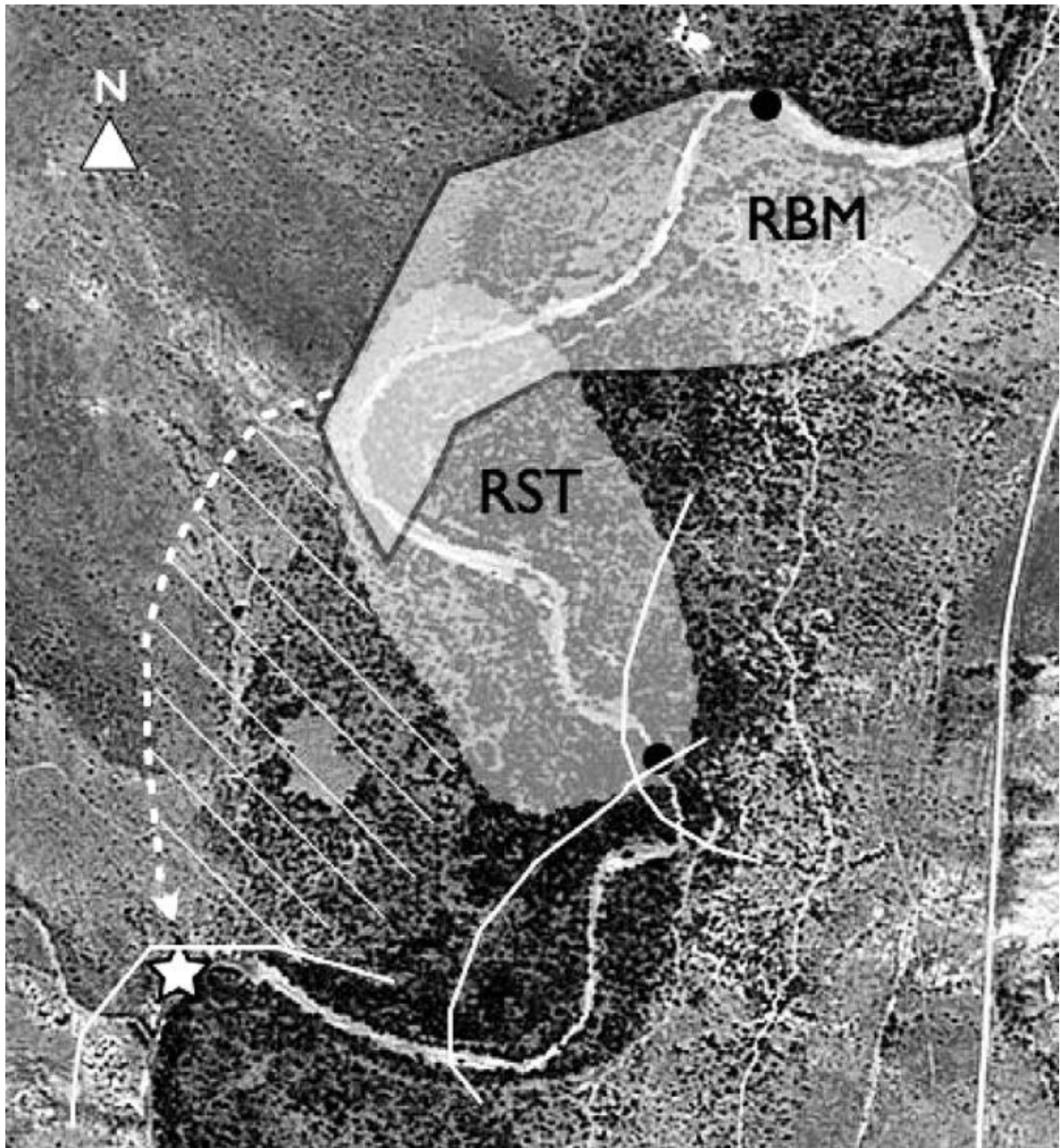
Figure 1. Aerial view of the study area indicating the boundaries of the RST and
RBM territories, along with the known boundaries of other troops in the area
(solid white lines). The locations of the last known water sources for the RST
and RBM are represented by black circles and the star represents the location of
the new water source. 1 cm = 100 m. Figure reproduced from McDougall et al.
(2010). Aerial photograph courtesy of Google Earth.

2.3 Analysis

2.3.1 Determination of troop hierarchy and steepness value

A troop dominance hierarchy was constructed from all decided agonistic interactions (i.e. active aggression which was not reciprocated, displacements, supplants, and submissive behaviours such as cowering). Agonistic interactions were collected *ad lib*. throughout the study period. A total of 1055 interactions were used to build the hierarchy, 4.6% of which were reversals (Table 1).

De Vries et al.'s (2006) modified version of David's score (DS: David, 1988), which corrects for the number of interactions recorded within each dyad, was used to assess individual dominance ranks and steepness of the hierarchy.

2.3.2 Determination of association index

Rates of association were determined using a modified version of Silk et al.'s (2006a) composite sociality index. Although grooming and proximity have often been used to indicate the strength of social relationships (Cords 1997; Silk et al., 2006a), in many circumstances grooming is also used as a bargaining tool in a biological marketplace (Barrett et al., 2002; Gumert, 2007; Port et al., 2009). Therefore grooming may not be exclusively indicative of a strong social bond, but rather, the choice of grooming partners may also be dependent on current "market trends". For example, Barrett and colleagues (2002) found that grooming was reciprocated more often during times of low foraging competition, whereas an increase in foraging competition led to a higher prevalence of grooming up the hierarchy. Due to this effect, it has been suggested that measures of grooming are not always an accurate indicator of social bonds (Barrett & Henzi, 2002;

Henzi & Barrett, 2007). Also, because grooming bouts are often long in duration and infrequent throughout the day, sampling biases can easily be introduced through the recording of these grooming episodes.

In the current study, I first determined the grooming index and the proximity index using Silk et al.'s (2006aa) method (grooming index: G_{ij}/G_{xy}; proximity index: P_{ij}/P_{xy}, where the first term is the frequency of grooming (G) or proximity (P) for dyad i,j and the second term is the average frequency of G or P for all dyads in the study period). However, a composite sociality index was not obtained (i.e. adding these values together, and then dividing by two, to obtain a combined value which weights both measures equally). Instead, the grooming and proximity indexes were then compared for each dyad and it was noted whether their values corresponded to the same category (associate, neutral, or non-associate). Only 49.9% of the grooming and proximity values coincided (n=407), thus it was concluded that the proximity sociality index alone would provide a more accurate measure of the strength of social bonds for this study troop. Nevertheless, at the suggestion of an anonymous reviewer, an additional analysis using only the grooming sociality index was carried out. The results of this analysis and its implications are presented in the Appendix.

The category 'associate' refers to those dyads with a proximity sociality index within the top 40% of all dyads (i.e. those dyads with a score > 1.0), and likewise, non-associates have a proximity sociality index within the bottom 40% of all dyads (i.e. those dyads with scores < 0.8). Dyads with proximity index scores between 0.8-1.0 (which corresponds roughly to the range of scores between the median and the mean average for all dyads) were considered neutral (Figure 2).

Table 1. Hierarchy matrix for the riverside troop (RST)

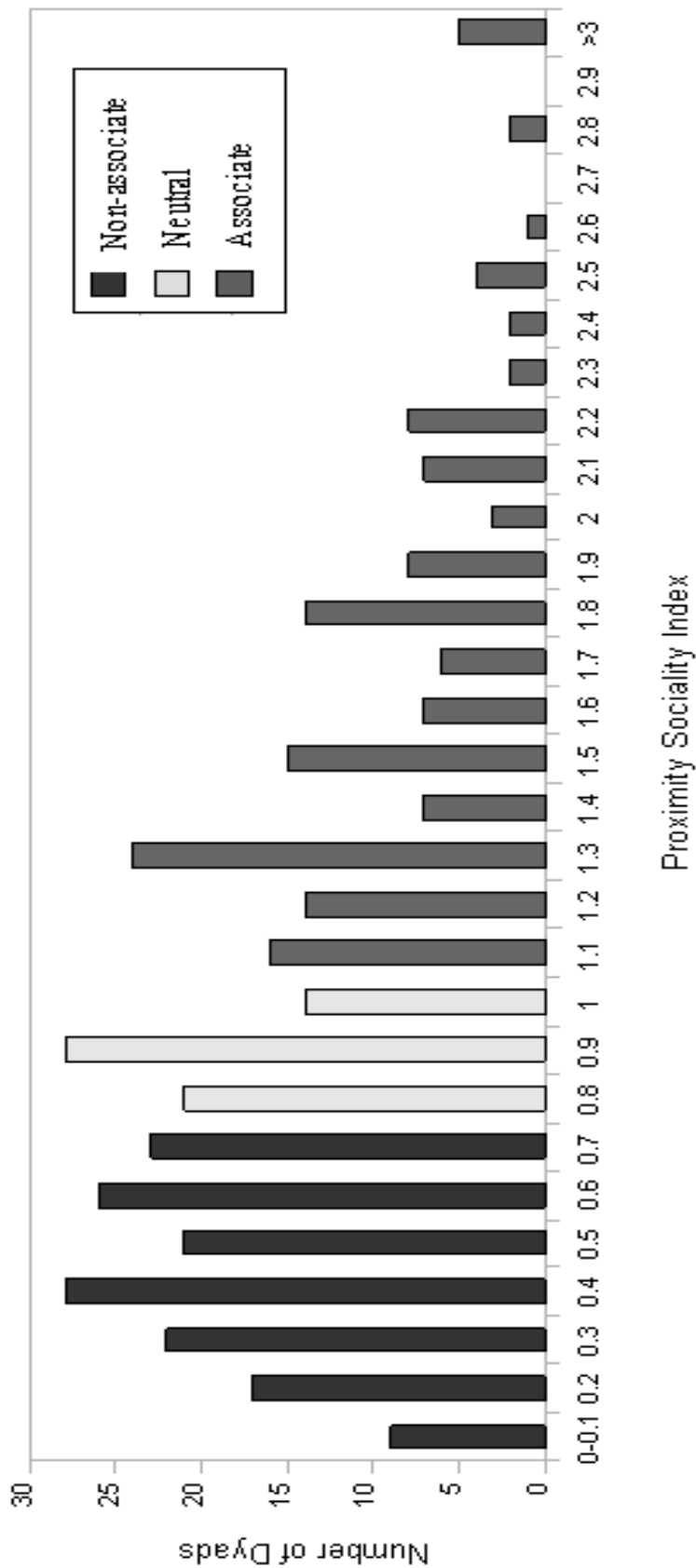|	Sm	Me	PJ	Iz	Al	Wi	Do	He	El	Cl	Um	Ni	Ru	Te	Gl	Xa	Vv	Zi	Li	Je	Fe	Ki
Sm		5	3	12		3	2	2	2	2	1	2	2	9	5			8	2	2	8	3
Me	1		6	10	2	6	3	3		3	2	1	2	2	3			6	4	3	8	4
PJ		4		12	1	8	9	2	9	9	1	2	1	6	4			7	8	5	10	9
Iz	1	4	11		21	6	9	3	9	10	2	3		7	5			2	6	3	18	10
Al				6		4	5											4	2			3
Wi	1						2	1										10	7	3	10	
Do	1							14										4	15	4	9	1
He						1												2	12	9	10	11
El																		4	1	1		1
Cl																		9	2	3	8	
Um																		7	4	1	1	2
Ni																		20	3	12	8	6
Ru	1	1	1																13	3	10	9
Te																			17	8	10	15
Gl																			2	3		4
Xa																		1	2	2		2
Vv																			1	3	4	1
Zi																			2	8	2	2
Li																				25	17	24
Je																			2		8	3
Fe																			1			14
Ki																			1	1		

Figure 2. Distribution of proximity sociality index scores for 341 dyads. The median sociality index is 0.8 and the mean is 1.0. All dyads between the median and mean were considered neutral and were not included in analyses involving rates of association.

Chapter 3

SCRATCHING OUR HEADS: RETHINKING SOCIAL ANXIETY IN VERVET MONKEYS

Abstract

Numerous conflicting results exist in the primate literature regarding the role of dominant individuals in creating conditions of social anxiety. Self-directed behaviours (SDB) have been used as an indicator of increased anxiety in primates to examine the effects of social stimuli such as dominance and association. This study recorded SDB from 11 free-ranging female vervet monkeys in the semi-arid Klein Karoo region of South Africa for a total of 468 focal hours to determine whether anxiety was influenced by the hierarchical rank of, and degree of association with, neighbouring monkeys. Associates were those dyads that spent long periods of time together (i.e., proximity sociality index scores in the top 40% of all scores) and non-associate dyads spent very little time together (i.e., scores within the bottom 40% of all scores). Rates of SDB were significantly higher when dominant neighbours were non-associates as compared to associates. The rate of SDB when neighbours were dominant associates vs. subordinate associates did not differ. These findings indicate that anxiety is influenced to a greater extent by the degree of association with neighbouring monkeys than by hierarchical rank. Measurement of multiple social variables can elucidate the relative contributions of the variables to changes in SDB and demonstrate how the variables interact, thereby providing a more comprehensive understanding of conditions leading to changes in social anxiety.

Keywords: **Self-directed behaviour, vervet, social anxiety, dominance, association**

3.1 Introduction

In individualized societies - where group members recognize each other, remember past interactions, and encounter each other on a regular basis - the levels of anxiety experienced while in proximity to particular individuals can vary widely. Self-directed behaviours (SDB) are commonly used to investigate anxiety levels, because they correlate with situations of apparent stress (e.g., during and immediately following agonistic interactions), with administration of pharmacological drugs to increase or decrease anxiety, as well as with subjective ratings of anxiety (Maestripieri et al., 1992; Spruijt et al., 1992; Schino et al., 1996; Troisi, 2002). However, the results of these studies have often produced discrepancies. For example, female chimpanzees (*Pan troglodytes*) increased their SDB when in proximity to an individual with whom they spent very little time (Kutsukake, 2003). Female white-faced capuchins (*Cebus capucinus*), on the other hand, increased their SDB when in proximity to animals with which they spent the most time (Manson & Perry, 2000). Some conflicting results may be attributable to methodological differences because data collection protocols designed for highly social terrestrial species may not be compatible with those for arboreal primates or species who seldom engage socially. However, it may also be that differences in social structure (e.g., tolerance) result in very different anxiety eliciting situations.

Species' differences in the level of tolerance (Sterck et al., 1997) exhibited by group members may account for some of the discrepancies in SDB research, as female

chimpanzees, with high levels of social tolerance and often indistinguishable hierarchies, were unaffected by neighbours of a higher rank (Kutsukake, 2003), while members of species characterized by low tolerance and strict, linear dominance hierarchies (Sterck et al., 1997) experienced an increase in anxiety when approached by a dominant individual (e.g. rhesus macaques (*Macaca mulatta*): Aureli et al.,1999; olive baboons (*Papio anubis*): Castles et al., 1999). Vervet monkeys (*Chlorocebus aethiops*) have been classified as resident nepotistic (Sterck et al., 1997) and data from east African vervets indicates that they have strict, linear hierarchies with steepness values between 0.99 and 1.00 (Seyfarth, 1980; Schino & Aureli, 2008). In resident nepotistic societies, aggression from dominant individuals is expected to result in an increase in SDB while in proximity to higher-ranking neighbours (Aureli et al., 1999; Castles et al., 1999; Daniel et al., 2008). Recent evidence, however, has shown that captive vervets did not change their rate of SDB when dominant neighbours were present (Daniel et al., 2008), a finding inconsistent with the suggestion that interspecies differences in degree of tolerance could explain variation in SDB in response to dominant neighbours (Kutsukake, 2003).

I investigated the effects of hierarchical rank and level of association of the neighbours in proximity on the rate of SDB in free-ranging female vervet monkeys to determine how anxiety is influenced by these two variables. If the vervet monkeys of South Africa's Klein-Karoo are indeed characterized by strict hierarchies and low levels of tolerance, I predicted that they will show an increase in SDB when in proximity to dominant individuals due to high rates of aggression received from them. Alternatively, low hierarchy steepness values in this population may indicate interpopulation variation in

vervet social structure and thus caution against intraspecific generalization of results from other populations. The second aim of this study is to investigate whether patterns of association with neighbours also contributes to variation in a female's level of anxiety. Although low levels of affiliation and association correlate with an increase in SDB (macaques: Schino et al., 1990; chimpanzees: Kutsukake, 2003), the reason for this behaviour remains unclear. The correlation between SDB and association time would appear to be of particular importance if the group is low in cohesiveness (e.g., chimpanzees: Kutsukake, 2003), or if it is very large, both of which would result in low levels of interaction between some of the dyads within the group. Uncertainty regarding another's behaviour can increase anxiety (Miller, 1997; Silk, 2002b); therefore, familiarity may lead to greater predictability of behaviour and consequently decrease anxiety (Kutsukake, 2003). It may also be; however, that other differences exist between associates and non-associates, such as rate of aggression. If aggression is received primarily from dominant non-associates it will demonstrate a link between dominance and association, and indicate that rates of aggression may explain more of the variation in SDB than dominance rank alone.

3.2 Methods

3.2.1 Study Site
The study site is situated in the semi-arid Klein Karoo of South Africa (32º 22`S, 24º52`E) at an altitude of 846m. With a mean annual rainfall of 330 mm, most of the

surrounding area is uninhabitable by vervets apart from the woodland surrounding drainage-line riverbeds. These riverbeds only flow in times of heavy rain in their catchment area, but nonetheless contain fairly permanent pools of water throughout most of the year (c.f. McDougall, et al., 2010). The woodland surrounding the milk river, where the focal study troop resides, is dominated by acacia (*Acacia karoo*), Karee (*Rhus lancea*), and Peruvian pepper (*Schinus molle*), all of which are primary food sources.

3.2.2 Subjects

I collected data from October 2008 to June 2009 from a single troop of free-ranging vervet monkeys. Habituation and identification of all adult and sub-adult troop members occurred in the six weeks prior to the start of data collection. Individuals were visually recognizable from a combination of characteristic facial features, coat color, body size, tail posture/length and scars/wounds to the face, ears, body and/or tail. Troop size was approximately 70 individuals. This included 22-24 adult and sub-adult females and 13-18 adult and sub-adult males. 13 infants were born between October and November 2008. Sub-adults were counted as those who participated in the 2009 breeding season, but in the case of females, did not yet have elongated nipples (indicative of nursing offspring), and in the case of males, were larger than adult females, but not yet adult sized.

To ensure that human presence would not influence their levels of anxiety, I chose the 11 most habituated females in the troop as focal subjects. Monthly rates of SDB when the observer, but no conspecifics, were in proximity were plotted and compared across time to ensure that all 11 individuals were adequately habituated prior to the start of data

collection. Monthly rates of SDB in relation to observer presence indicated a slight declining trend over the duration of the data collection period (linear regression: r^2=0.082, B= -0.012, β= -.287, p=0.007), suggesting that any noise added to the data as a result of my presence was not likely a confounding factor in the analysis. Two of the 11 females showed elevated levels of SDB until December 2008, at which time they decreased to a steady rate for the remaining seven months. These elevated levels of SDB were accompanied by behaviours that made it difficult to collect data from these individuals accurately (e.g., running from the observer, hiding in a tree top or acacia thicket). These behaviours diminished at the same time that SDB rates reached a steady rate, therefore these two individuals were not considered 'habituated' until December 2008 and data prior to this time were excluded from analysis (Table 2).

Table 2. Subjects for focal samples.

Identification	Reproductive state*	Rank	Months sampled	Time sampled (minutes)
DO	L(2007 infant)	7	October 2008 – June 2009	2557
FE	X	21	October 2008 – June 2009	2608
HE	P,L	8	November 2008 – June 2009	2520
IZ	X	4	October 2008 – June 2009	2555
JE	P,L	20	November 2008 – June 2009	2514
KI	P,L	22	October 2008 – June 2009	2414
LI	P,L	19	November 2008 – June 2009	2601
NI	X	12	December 2008 – June 2009	2637
RU	X	13	December 2008 – June 2009	2560
TE	P,L	14	October 2008 – June 2009	2536
ZI	X	18	November 2008 – June 2009	2566

* L=lactating, P=pregnant, X=not pregnant or lactating

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3.2.3 Data collection

I followed the monkeys on foot for 10 hours per day. Daylight hours were divided into four equal time blocks and focal samples from each female were distributed evenly across the time blocks. The same subject was not followed more than once per day in each time block. The length of each time block fluctuated between 2.5 and 3.5 hours depending on the seasonal photoperiod. Focal samples were 20 minutes in length from October 2008 through to March 2009, and were 30 minutes in length after that. A focal sample was terminated if an individual went out of sight for more than 5 minutes. I used a Palm Tungsten^{TM} E2 Handheld using Pendragon 5.1 (2005-2007) software for collecting data. Hierarchy data were collected *ad lib*. and all other data were collected during focals using continuous and instantaneous sampling methods (Altmann, 1974). An instantaneous sample was collected at the start of every focal animal follow and every two minutes throughout. These samples included a record of the ID of all adult and sub-adult individuals within the focal animal's five meter radius (hereafter referred to as neighbours).

Self-directed behaviours (SDB) were recorded continuously during focal animal follows according to the following categories:

1) Scratch – the fingertips of the hand or foot are drawn across the fur/skin of the body in a repetitive motion.

2) Self-groom – examining various body parts or slowly brushing through their hair and picking at the skin with one or both hands.

3) Body/head shake – shaking of the head and neck, sometimes followed by shaking of the entire body.

4) Yawn – tilting the head back and gaping the mouth.

A new SDB was recorded any time an individual switched to a new class of SDB or if there was a break of >5 seconds between bouts (for scratching and self-grooming). Each time a SDB was scored, the IDs of all neighbours were recorded in the same fashion as that of the instantaneous samples.

Aggression was also recorded continuously during focal animal follows and classified according to the following categories:

1) Displacement - change of location in response to the movement and/or posture of the aggressor.

2) Supplant - take-over of an activity and spatial location by the aggressor.

3) Eyebrow raise – the aggressor's ears are pulled back and eyebrows raised, causing a tightening of the facial skin and displaying the pink skin above the eyes.

4) Lunge – a quick, sudden movement by the aggressor in the direction of the recipient, causing a displacement or cower by the recipient.

5) Chase – the aggressor moves quickly and directly towards the recipient and does not stop once the recipient begins to move. This behaviour generally lasted between 2 sec and several minutes.

6) Attack – physical contact between the aggressor and recipient including such acts as: biting, scratching, or grabbing by the aggressor.

3.2.4 Analysis

I constructed a troop dominance hierarchy from all decided agonistic interactions (i.e. non-reciprocated aggression that included a clear winner). De Vries et al.'s (2006)

modified version of David's score (DS: David, 1988), which corrected for the different number of interactions recorded within each dyad, was used to assess individual dominance ranks and steepness of the hierarchy.

I used the amount of time that a dyad spent in proximity (within 5m) to classify dyads as associate, neutral, and non-associate, as a proxy for the strength of their social relationship (Cords, 1997; Silk et al., 2006a). A modified version of Silk et al.'s (2006a) composite sociality index was used to compute a proximity sociality index (proximity index: P_{ij}/P_{xy}, where the first term is the frequency of proximity (P) for dyad i,j and the second term is the average frequency of P for all dyads in the study period). A composite sociality index (i.e., one that combines the rate of proximity and grooming) was not used due to potential pseudo-replication of the grooming data. 'Associates' have a proximity sociality index within the top 40% of all dyads (i.e. scores > 1.0) and 'non-associates' have a proximity sociality index within the bottom 40% of all dyads (i.e. scores < 0.8). Dyads with proximity index scores between 0.8-1.0 (which corresponds roughly to the range of scores between the median and the mean average for all dyads) were considered neutral (Figure 2).

Next, I determined the rate of SDB performed per minute for each condition (i.e. when the neighbours were exclusively a) dominant non-associates, b) dominant associates, or c) subordinate associates). This was done for each test female by dividing the total number of SDB that occurred when in proximity to a particular class of individuals, by the total amount of time spent in proximity to the same class of individuals (for example,

under condition x: $SDB_x/(\text{scan samples}_x*2)$. A rate of SDB could not be determined for

when the neighbours were exclusively subordinate non-associates due to several low

ranking females (n=5) not having any subordinates who were non-associates, and two

higher ranking females which did not spend any time with subordinate non-associates.

Additionally, the rate of SDB when the focal individual was alone (i.e. no adults or sub-

adults within 5m) was determined for each focal female and this was considered her

'baseline' value. The rate of SDB in each of the proximity conditions was then

subtracted from the baseline rate of SDB for each female to obtain a change in rate of

SDB. This change from baseline rate of SDB was used as the comparison value for each

of the proximity conditions. The three conditions were then compared using a repeated

measures ANOVA. Post-hoc pairwise comparisons were conducted using Wilcoxon-

Signed Ranks tests with a Bonferroni adjustment for multiple comparisons.

Rates of aggression received from dominant associates and dominant non-associates were

corrected for the amount of time spent in proximity by totaling the number of aggressive

bouts received and dividing by the amount of time spent in proximity. The corrected

rates of aggression from dominant associates and dominant non-associates were then

compared using the Wilcoxon signed-ranks test to determine whether the risk of

aggression from these two groups of individuals differed.

Finally, to ensure that a female's current reproductive state was not influencing her rate of

SDB in response to the presence of particular individuals, I conducted an independent

samples T-test comparing the females in each reproductive state. The change in SDB for

each condition (i.e., the exclusive presence of a) dominant non-associate, b) dominant associate, or c) subordinate associate neighbours) was compared for females who were pregnant or lactating (n=6) and those who were in neither state (n=5).

3.3 Results

3.3.1 General Rates of SDB

The mean (± SEM) overall rate of SDB for the 11 focal females was 0.28 ± 0.02 bouts/min. These females had at least one neighbour (adult or sub-adult) 44% of the time and no difference in the rate of SDB was found in the presence or absence of neighbours (Wilcoxon signed-ranks test: T=33, n=11, p=1.000; mean = 0.28 vs. 0.29 SDB/min).

3.3.2 Effects of Association and Dominance

The female dominance hierarchy had a steepness value of m=0.66 (where m is the slope of the line (y=mx+b) describing the distribution of normalized David's Score (DS) values for females in the troop). Solo females were never observed to win dominance interactions with adult males, therefore all adult males were considered higher ranking than adult females.

The dominant associate, dominant non-associate, and subordinate associate conditions differed significantly (repeated-measures ANOVA with a Greenhouse-Geiser correction F=18.16, df=1.13, p=0.001). The mean change in rate of SDB from baseline (± SEM) for each condition is given in figure 2. Pairwise comparisons revealed a significant difference in the rate of SDB when neighbours were dominant associates vs. dominant

non-associates (mean difference=0.138, p=0.009), as well when neighbours were dominant non-associates vs. subordinate associates (mean difference=0.161, p=0.004). There was no difference in the rate of SDB when neighbours were dominant associates or subordinate associates (mean difference=0.023, p=0.148). A test of between-subject effects showed that there were no significant differences between subjects (F=0.25, df=1, p=0.627)(Figure 3).

The grooming sociality index produced the same results (i.e. the rate of SDB differed significantly between dominant non-associate neighbours and both the dominant associate and subordinate associate neighbours, while the latter two classes did not differ from each other); however, due to potential pseudo-replication of the grooming data, only the proximity data are presented here (see appendix for further information regarding the grooming sociality index).

3.3.3 Rates of Aggression

Aggression received from dominant associates (mean ± SEM: 0.037 ± 0.003) was significantly lower than aggression received from dominant non-associates (0.069 ± 0.011) (Wilcoxon signed-ranks test: T=8, n=11, p=0.026).

3.3.4 Effects of Reproductive State

There were no differences in the rate of SDB between the two reproductive classes for dominant non-associate neighbours (t(9)=0.64, p=0.536), dominant associate neighbours (t(9)=1.72, p=0.119), or subordinate associate neighbours (t(8)=0.90, p=0.395).
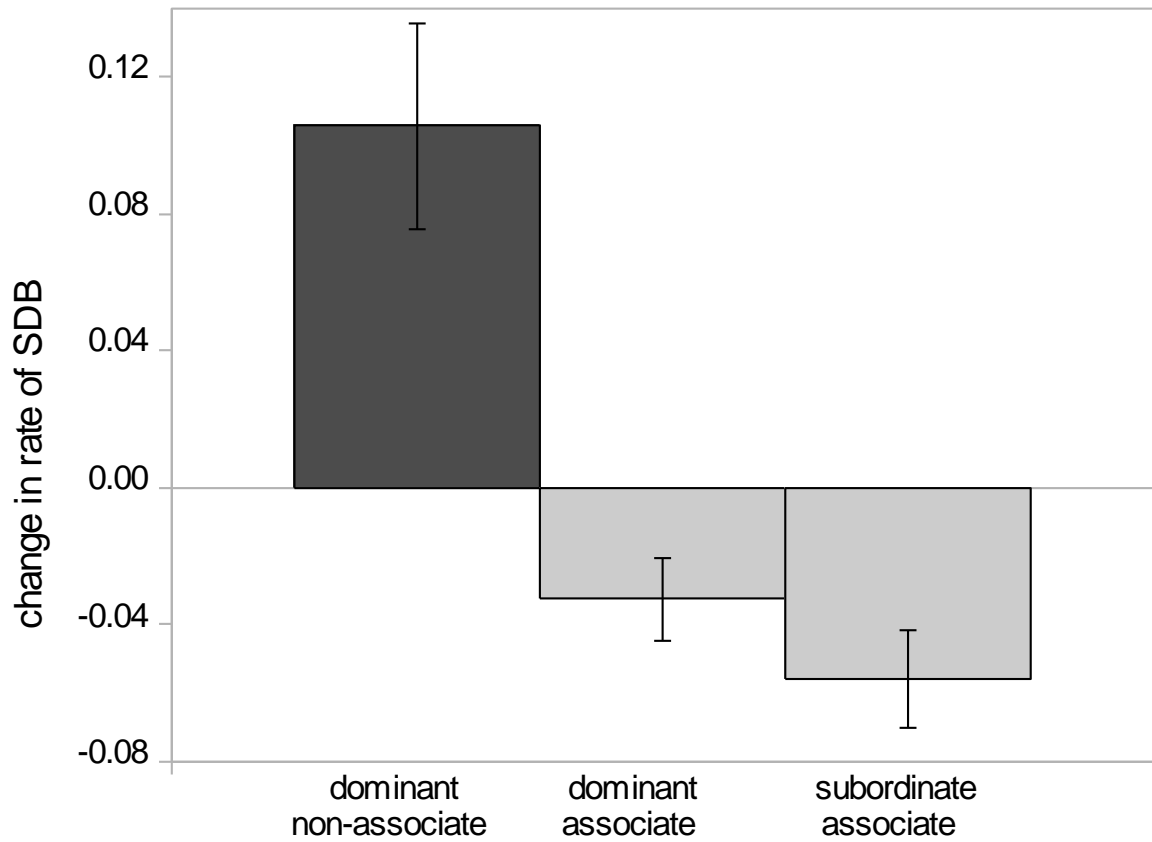
Figure 3. Bars indicate the mean (± SEM) change in the rate of SDB when focal females had neighbours that were dominant non-associates, dominant associates, or subordinate associates. The change in rate of SDB is calculated as the deviation from their baseline value (i.e. when they were alone).

3.4 Discussion

I observed no change in anxiety, as measured through SDB, when an individual was alone or when they had a conspecific within five meters of them. The rate of SDB did, however, change significantly when neighbours were categorized according to rank and degree of association. SDB were significantly higher when neighbours were dominant non-associates as compared to when neighbours were dominant associates, or subordinate associates. When adjusted for amount of time spent in proximity, aggression was received more frequently from non-associates as compared to associates. Finally, there was no indication that the change in rate of SDB associated with the presence of particular classes of individuals (i.e. dominant non-associates, dominant associates and subordinate associates) was influenced by a female's current reproductive state.

Neighbour association appeared to override the effects of dominance, as neighbours who were dominant but also associates decreased the focal individual's rate of SDB from baseline. This finding, however, may not apply to all vervet monkey populations. Indeed, the steepness value obtained in this study troop (0.66) was very low in contrast with the steepness values obtained from several troops of East African vervets, which ranged from 0.99 to 1.00 (Seyfarth, 1980; Schino & Aureli, 2008). The steepness of these hierarchies, in combination with small troop sizes (which likely produces less variation in rates of association between dyads and a greater degree of kinship between individuals in the troop) could produce results in direct opposition to the ones presented here. Recent findings from a relatively small (n=10) troop of captive vervets, however, were in agreement with the present study, indicating a hierarchy steepness value of 0.60

and no change in SDB with proximity to dominant individuals, although the effects of association were not considered (Daniel et al., 2008). Interspecific differences in the degree to which neighbour dominance influences anxiety are suggested to be attributed to variation in the level of tolerance exhibited between members of a particular species (Kutsukake, 2003), and it seems likely that this hypothesis extends to intraspecific variation as well. In addition to vervets, high variation in hierarchy steepness values are evident in Japanese macacues, *Macaca fuscata* (with values ranging from 0.07 to 0.99), mantled howler monkeys, *Alouatta palliata* (0.26 to 0.67), and tufted capuchins, *Cebus apella* (0.42 to 0.81) (Schino & Aureli, 2008). Accordingly, measures of tolerance, such as the steepness of hierarchy measure used here (de Vries et al., 2006), can assist in determining the contribution of dominance to social anxiety both across and within species.

Results indicated differences in the rate of SDB only when the neighbour's association classification changed (i.e. dominant non-associates differed from both dominant associates and subordinate associates), whereas no difference in the rate of SDB was found when the neighbour's rank classification changed, but the degree of association did not (i.e. dominant associates and subordinate associates did not differ). These findings question the idea that the increase in anxiety is the result of aggression from dominant individuals (Aureli et al., 1999; Castles et al., 1999; Daniel et al., 2008) because an increase in SDB did not accompany proximity to dominant associates, despite receiving aggression from these individuals. The adjusted rate of aggression received from dominant individuals, however, may explain changes in anxiety to a greater extent than

mere aggression or dominance alone. Furthermore, it may be that degree of association is correlated with risk of aggression, as the adjusted rate of aggression was significantly higher from dominant non-associates than dominant associates. Kin-selection is likely to play a role in producing this effect because female associates are often kin (Silk et al., 2006a; Silk et al., 2006b) and aggression within kinship groups is less damaging to relationships (Bergman et al., 2003) and therefore presumably less anxiety inducing. Data on kinship were not available to test this hypothesis in the current study, although it should be noted that an average of 46% of a female's associates were adult or sub-adult males, and thus not likely kin (owing to the female philopatric nature of this species (Struhsaker, 1967; Cheney & Seyfarth, 1983)). With a larger data set, it may be possible to tease apart the effects of sex and kinship within each classification, as it may be that a particular group of individuals (e.g. dominant, female, non-kin, non-associates) are responsible for the majority of aggression, and subsequently, may be solely responsible for increases in SDB in the focal animals. If this is the case, changes in anxiety cannot be attributed to any one characteristic, but rather, to a particular combination of characteristics possessed by a neighbouring monkey.

The results presented here suggest that an increase in SDB while in proximity with non-associates may be induced by an increased risk of aggression; however, there is also the possibility that behavioural predictability contributes to this effect. It has been suggested that a reduction in the ability to predict the behaviour of others leads to an increase in anxiety (Aureli & van Schaik, 1991; Miller, 1997; Castles & Whiten, 1998; Das et al., 1998; Silk, 2002a; Silk, 2002b), and as such, familiarity with particular troop members

(as measured in the current study through time spent in proximity) allows for more accurate prediction of behaviour and a reduction in anxiety while in proximity with these individuals (Schino et al., 1990). An examination of rates of SDB in response to subordinate associates and non-associates (thereby reducing or eliminating any effects of increased risk of aggression on SDB) would provide insight into the contribution of predictability on rates of SDB. Limitations of the present data set prevented a complete analysis of subordinate neighbours; nevertheless, the trend replicated the findings obtained from dominant neighbours (i.e. SDB were lower when in proximity with subordinate associates (mean ± SEM: 0.22 ± 0.02) as compared to subordinate non-associates (0.34 ± 0.05)), suggesting that association may be influencing anxiety independent of aggression rates. Future studies with larger data sets would thus be beneficial in verifying these results.

The research presented here suggests that anxiety can be understood more precisely by examining how social variables interact and investigating their relative contributions to influencing rates of SDB. More specifically, dominance alone does not appear to be a good indicator of changes in SDB in this population, but remains a useful measure in combination with association and aggression data. These results have implications for how we approach the study of emotion and social relationships and indicate that the response to a social partner may be the result of a unique combination of variables that characterize a particular dyad.

Chapter 4

KEEPING AN EYE ON THINGS:

NEIGHBOUR SPATIAL LOCATION INFLUENCES AROUSAL IN VERVET

MONKEYS.

Abstract

The presence of particular social stimuli (e.g. dominant or unfamiliar individuals) has been demonstrated to influence the degree of arousal an animal experiences. It is not clear, however, how the animal's current focus of attention influences arousal under these social conditions. Self-directed behaviours (SDB) were used as an indicator of arousal in free-ranging vervet monkeys (*Chlorocebus aethiops*) to determine whether arousal varied dependent on a neighbour's spatial location (used as a proxy for direction of attention). 468 hours of focal data were collected from 11 free-ranging female vervet monkeys inhabiting the Karoo region of South Africa. A female's rate of SDB when her nearest neighbour was located behind her was significantly lower than when she was alone or when her nearest neighbour was within her visual field (i.e., to the front, side, above or below). This trend held regardless of neighbour dominance status. These results are consistent with the hypothesis that female vervet monkeys are behaviourally influenced by nearby neighbours that are not visually salient, and that they may only turn their back to their nearest neighbour when the need for social monitoring is low. In accordance with the theory of social affordances, this research also suggests that socially arousing stimuli does not appear to induce arousal when it is located behind the individual and is thus not likely to be the current focus of attention.

Keywords: **Self-directed behaviour, vervet monkey, social arousal, spatial perception, attention, neighbour location, affordances.**

4.1 Introduction

Emotions can be viewed as an evolved mechanism for cataloguing past interactions/events, and thus provide an expedient 'rule of thumb' as to how an individual should respond in a given situation (Aureli & Schaffner, 2002) . Emotions can therefore act as an intervening variable, integrating past and present information to create an overall emotional perception of the current situation, and subsequently influence the behavioural outcome. According to Bradley and Lang (2000), emotions are comprised of three basic components: behaviour, feeling, and physiology. Although the mentalistic 'feeling' component of an emotion is difficult, if not impossible, to measure objectively in non-human animals, investigating the behavioural and physiological aspects of emotional responses to particular social scenarios could provide valuable information as to the nature of the relationship between two individuals and their likely historical patterns of interaction, in addition to the potential outcome of the event.

One behavioural indicator of emotion that has been used widely among primates is displacement activities, or so-called self-directed behaviours (SDB) (Maestripieri, et al., 1992; Troisi, 2002). SDB are behaviours such as scratching or self-grooming that increase in frequency during or immediately following periods of increased arousal and act to counterbalance the stimulating effects of arousal through the production of endorphins (Spruijt, et al., 1992). Indeed, pharmacological evidence has demonstrated a correlation between changes in the rate of SDB and the administration of anxiogenic or anxiolytic drugs (Schino, et al., 1996), and behavioural studies have indicated an increase in SDBs immediately following anxiety eliciting social situations such as bouts of

aggression (Aureli, 1992; Aureli & Van Schaik, 1991; Castles & Whiten, 1998; Das, Penke, & van Hooff, 1998).

SDBs have therefore been used to examine a range of social contextual variables such as changes in arousal pertaining to aspects of individual relationships (e.g., rank effects and degree of association: Castles, et al., 1999; Daniel, et al., 2008; Kutsukake, 2003; Manson & Perry, 2000; McDougall, In-press), differing social systems (i.e., across species: Kutsukake, 2003), and particular social situations (i.e., across time: Aureli & Van Schaik, 1991; Castles & Whiten, 1998). No study to date, however, has used SDBs to examine the effects of arousal pertaining to an individual's perception of their 'social space', i.e., the three-dimensional "field" in which interactions take place. Here, I examine how the spatial location of an individual's nearest neighbour influences their level of arousal and I place this in the context of social perception and the theory of affordances (Gibson, 1979).

The ability to engage in a particular behaviour is dependent on an animal's capability to *perceive* opportunities and possibilities for action; these are termed "affordances" (Chemero, 2003; Gibson, 1979). For example, a vervet may perceive an acacia flower as affording eating, whereas a jackal's perception of the flower will not provide the same possibility for action. Simply put, the affordances of the environment for a particular individual will regulate the behavioural repertoire that can be expressed in that environment (Reed, 1996). Affordances also have implications in the social realm, such that the perception of another individual is linked to a set of possible social actions.

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Thus, in socially complex societies such as those of many diurnal primates, the social environment is generally a stimulating one full of possibilities for action (Barrett & Rendall, 2010). In the current study, I address the question of what happens when a monkey's neighbour is located behind them (i.e. is not the current focus of their attention), and therefore does not afford opportunity for social engagement.

Head and body orientation provide a good indicator as to the focus of social attention (Emery, 2000; Langton, Watt, & Bruce, 2000), and social attention on the part of the initiator is a prerequisite for interaction. Social affordances would therefore not be expected to present themselves to an individual that is not in a position to be attentive to their neighbour. If social arousal (as determined by the animal's rate of SDBs) is increased due to the perceived affordances for social interaction provided by a nearby, visually salient individual, then a neighbour that is located behind the focal animal should not induce the same increase in arousal. Rather, the level of social arousal experienced when an animal's neighbour is positioned behind them is predicted to be similar to the level of arousal experienced when they are alone. This hypothesis will be tested in a free-ranging population of vervet monkeys (*Chlorocebus aethiops*) inhabiting the Karoo region of South Africa to investigate how an individual's perception of their three-dimensional social environment influences arousal.

4.2 Methods

4.2.1 Study Site

The study site is situated in the semi-arid Klein Karoo of South Africa (32º 22`S,

24º52`E) at an altitude of 846m. With a mean annual rainfall of 330 mm, most of the surrounding area is uninhabitable by vervets apart from the woodland surrounding drainage-line riverbeds. These riverbeds only flow in times of heavy rain in their catchment area, but nonetheless contain fairly permanent pools of water throughout most of the year (c.f. McDougall, et al., 2010). The woodland surrounding the milk river, where the focal study troop resides, is dominated by acacia (*Acacia karoo*), Karee (*Rhus lancea*), and Peruvian pepper (*Schinus molle*), all of which are primary food sources.

4.2.2 Subjects

Data were collected from October 2008 to June 2009 from a single troop of free-ranging vervet monkeys. Habituation and identification of all adult and sub-adult troop members occurred in the six weeks prior to the start of data collection. Individuals were visually recognizable from a combination of characteristic facial features, coat color, body size, tail posture/length and scars/wounds to the face, ears, body and/or tail. Troop size was approximately 70 individuals. This included 22-24 adult and sub-adult females and 13-18 adult and sub-adult males. 13 infants were born between October and November 2008. Sub-adults were counted as those who participated in the 2009 breeding season, but in the case of females, did not yet have elongated nipples (indicative of nursing offspring), and in the case of males, were larger than adult females, but not yet adult size.

To ensure that human presence would not influence their levels of anxiety, the 11 most habituated females in the troop were chosen as focal subjects. Monthly rates of SDB when the observer, but no conspecifics were in proximity were plotted and compared

across time to ensure that all 11 individuals were adequately habituated prior to the start of data collection. Monthly rates of SDB in relation to observer presence indicated only a slight declining trend over the duration of the data collection period (r^2=0.082, B= -0.012, β= -.287, p=0.007), indicating that any noise added to the data as a result of my presence was not likely a confounding factor in the analysis and that focal individuals' levels of habituation remained fairly constant over the nine month period. Two of the 11 females showed elevated levels of SDB until December 2008, at which time they decreased to a steady rate for the remaining seven months. These elevated levels of SDB were accompanied by behaviours that made it difficult to accurately collect data from these individuals (e.g., running from the observer, hiding in a tree top or acacia thicket). These behaviours diminished at the same time that SDB rates reached a steady state, therefore these two individuals were not considered 'habituated' until December 2008 and data prior to this time were excluded from analysis (Table 2).

4.2.3 Data collection

The monkeys were followed on foot for 10 hours per day. Daylight hours were divided into four equal time blocks and focal samples from each female were distributed evenly across the time blocks. Data were not collected from the same focal subject more than once per day in each time block. The length of each time block fluctuated between 2.5 and 3.5 hours depending on the seasonal photoperiod. Focal samples were 20 minutes in length from October 2008 through to March 2009, and were 30 minutes in length after that. A focal sample was terminated if an individual went out of sight for more than 5 minutes.

Data were collected on a Palm Tungsten^{TM} E2 Handheld using Pendragon 5.1 (2005-2007) software. Data for the hierarchy were collected *ad lib*. and all other data were collected during focals using continuous and instantaneous sampling methods (Altmann, 1974). An instantaneous 'scan' sample was collected at the start of every focal animal follow and every two minutes throughout. These samples included a record of the ID and spatial location (i.e. front, behind, left, right, above, or below) of all adult and sub-adult individuals within the focal animal's five meter radius (hereafter referred to as neighbours). These six spatial locations project in a pyramidal fashion away from the focal individual such that they fill the five metre region of space around the monkey (Figure 4). Each spatial location is therefore mutually exclusive. The focal individual was considered to be alone when she had no adult or sub-adult neighbours within five meters of her.

Self-directed behaviours (SDB) were recorded continuously during focal animal follows. The following categorizations were used when scoring SDBs:

1) Scratch – the fingertips of the hand or foot are drawn across the fur/skin of the body in a repetitive motion.

2) Self-groom – examining various body parts or slowly brushing through their hair and picking at the skin with one or both hands.

3) Body/head shake – shaking of the head and neck, sometimes followed by shaking of the entire body.

4) Yawn – tilting the head back and gaping the mouth.

A new SDB was recorded any time an individual switched to a new class of SDB or if there was a break of >5 seconds between bouts (for scratching and self-grooming). Each time a SDB was scored, the focal animal's activity and the ID of all neighbours was recorded in the same fashion as that of the scan samples.
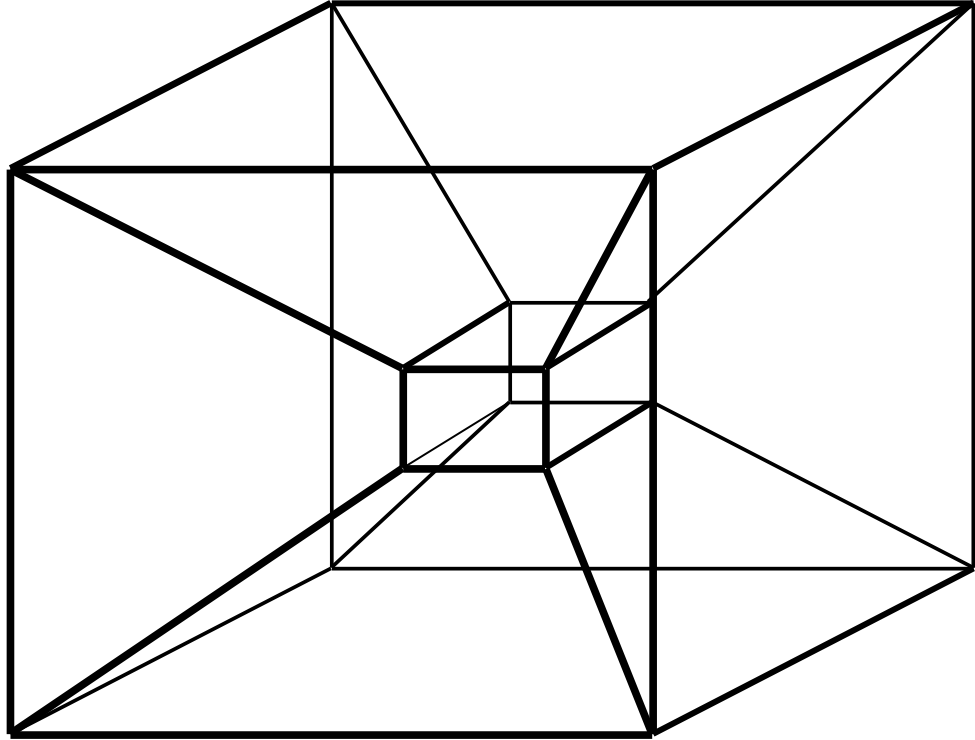
Figure 4. Three-dimensional schematic diagram of the six pyramidal regions of space surrounding a focal female. Although the five meter radius surrounding a female would form a sphere, the pyramidal projections have been depicted within a cube for ease of visual representation. The small cube in the centre represents the location of the focal individual.

4.2.4 Analysis

The rate of SDB for each condition (i.e. when the focal individual was alone, or when the nearest neighbour was in front, behind, above, below, or to the side of the focal individual) was determined for each test female. This was done by dividing the total number of SDB that occurred when her nearest neighbour was in a particular spatial region (or when there was no neighbour), by the total amount of time spent in the same condition (for example, under condition x: SDB_x/(scan samples$_x$*2).

The side condition (i.e. when the nearest neighbour was to the left or right of the focal female) was divided into its corresponding left and right components and compared using the Wilcoxon signed ranks test. The rates of SDB for each spatial location of the nearest neighbour (front, back, above, below, side) and the lone condition were then compared using a repeated measures Friedman test. Post hoc analyses for pairwise comparisons were performed using Wilcoxon signed ranks tests with an applied Bonferroni correction.

4.3 Results

4.3.1 Overall model

The mean overall rate of SDB for the 11 focal females was 0.28 SDB/min (95% confidence interval [CI] = 0.24, 0.32). The mean rate of SDB for each of the six conditions is given in Table 3. A comparison of the two components of the side condition (nearest neighbour to the left or right) indicated that SDB rate did not differ between the side on which the nearest neighbour was located (Wilcoxon signed ranks test: z= 0.089, p=0.929). The data for these two classifications therefore remained pooled within the

'side' location. The mean duration of time focal females spent with their nearest

neighbour in each of the six spatial locations is shown in Figure 5.

The Friedman test indicated that the rate of SDB differed significantly between

conditions ($X^2(6)=28.40$, $p<0.001$) and post-hoc pairwise comparisons using Wilcoxon

signed-ranks tests with an applied Bonferroni correction indicated that rates of SDB were

significantly lower when an individual's nearest neighbour was located behind her,

whereas the rate of SDB for all other nearest neighbour locations did not differ from each

other, nor from the rate of SDB when the female was alone (Table 4). Rates of SDB

when a female's nearest neighbour was located behind her were 45 % lower than when

she was alone (i.e. reduced by 0.13 SDB/min) (Figure 6).

Table 3. Mean (and 95% confidence interval [CI]) rate of SDB for each spatial location of nearest neighbour as well as when the focal female was alone (no one in her 5 m radius).

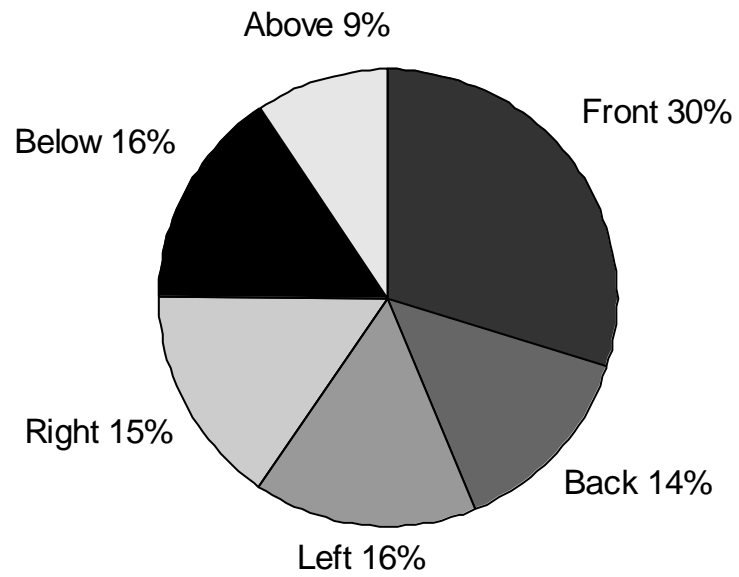| Spatial location of nearest neighbour	Mean rate of SDB	95% CI
Back	0.16	0.14, 0.18
Front	0.28	0.23, 0.33
Side	0.30	0.26, 0.34
Above	0.36	0.27, 0.45
Below	0.29	0.24, 0.34
No one	0.28	0.25, 0.31

Figure 5. Mean percentage of time focal females spent with their nearest

neighbour in each of the six spatial locations.

Table 4. Results of pairwise comparisons using Wilcoxon signed ranks tests with an applied Bonferroni correction. * The rate of SDB in the 'back' condition was significantly reduced from all other spatial locations.

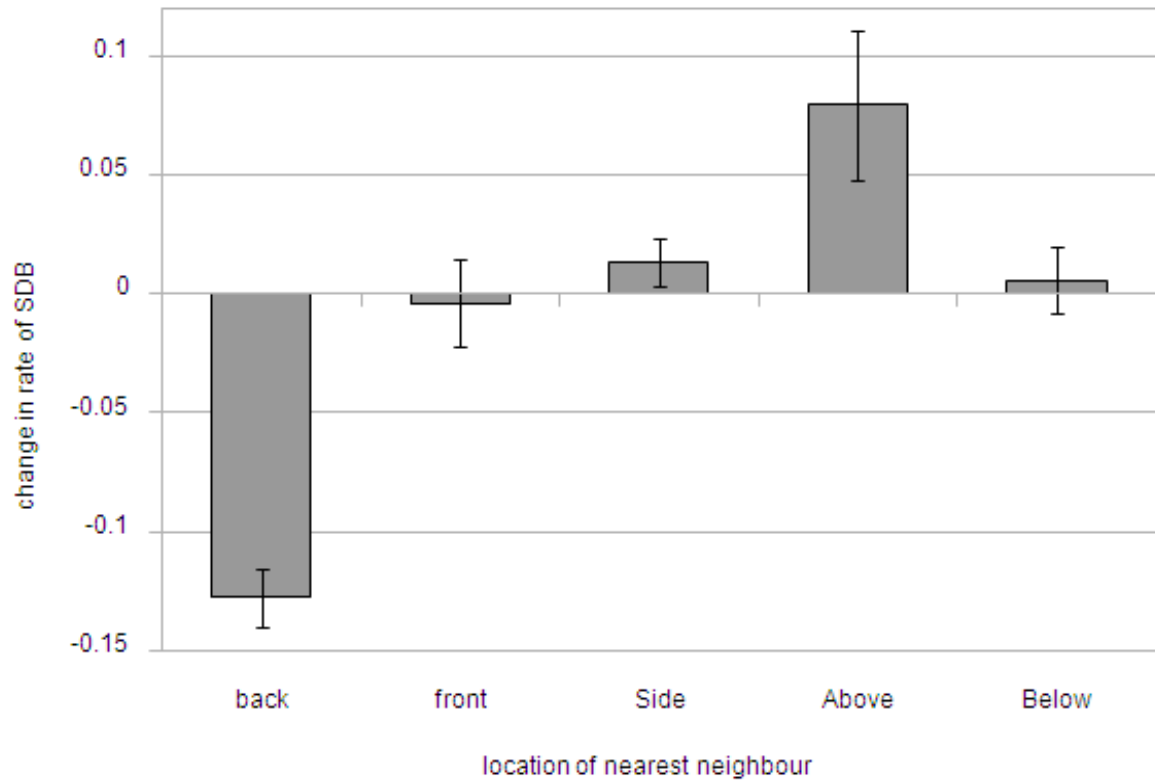|	No one	Above	Below	Side	Front	Back *
No one	X	Z=2.134, p=0.50	Z=0.45, p=1.00	Z=1.02, p=1.00	Z=0.27, p=1.00	Z=2.93, p=0.05
Above		X	Z=2.31, p=0.32	Z=2.05, p=0.62	Z=1.87, p=0.93	Z=2.93, p=0.05
Below			X	Z=0.45, p=1.00	Z=0.62, p=1.00	Z=2.93, p=0.05
Side				X	Z=1.07, p=1.00	Z= 2.93 p=0.05
Front					X	Z=2.93, p=0.05
Back						X

Figure 6. Mean (± SEM) change in rate of SDB for each nearest neighbour location. The changes in rate are with respect to the focal females' rate of SDB while she was alone (i.e. no neighbours within her 5 m radius). The only condition that differs significantly from all other is the 'back' location, which is significantly lower than all other conditions.

4.3.2 Post-hoc analyses and results

It is possible that dominance rank is a confounding factor for the decrease in SDB found when the nearest neighbour is behind the focal animal. For example, if dominant group members pose more of a threat than subordinate group members, then the presence of a dominant individual located behind a female may induce that female to orient towards them in order to monitor its behaviour more efficiently. This would then bias the sample of nearest neighbours in the 'back' condition if females leave their back turned only to non-threatening group members. I therefore classified nearest neighbours in the 'back' condition as either dominant or subordinate to the focal female and compared the rate of SDB for these two classes of neighbours using the Wilcoxon signed ranks test. Results indicated that there was no difference between the rate of SDB when the nearest neighbour behind the focal animal was dominant or subordinate (dominant: mean = 0.15; 95% CI = 0.11, 0.19, vs. subordinate: mean = 0.19; 95% CI = 0.12, 0.26, z=0.97, p=0.333). Additionally, I calculated the change in SDB when the focal animal was alone to when her nearest neighbour was located behind her for both dominant and subordinate neighbours and compared these two conditions using the Wilcoxon signed ranks test. Similarly, these results indicated no significant difference in the change in rate of SDB for dominant or subordinate individuals in the 'back' condition (dominant: mean = 0.14; 95% CI = 0.07, 0.21, subordinate: mean = 0.03; 95% CI = -0.04, 0.10, z=1.68, p=0.09). Finally, I calculated the time that dominant nearest neighbours were located behind the focal female as a proportion of the total duration of time that the nearest neighbour was dominant (i.e., duration of time with a dominant nearest neighbour in the 'back' condition / total duration of time with a dominant nearest neighbour) and compared this value to the

proportion of time subordinate nearest neighbours were located behind her. The
Wilcoxon signed ranks test indicated that focal females spent significantly longer periods
of time with their subordinate nearest neighbours located behind them as compared to
dominant nearest neighbours (dominant: mean = 0.13; 95% CI = 0.11, 0.15, subordinate:
mean = 0.16; 95% CI = 0.14, 0.18, z=2.05, p=0.04).

4.4 Discussion

Rates of SDB did not differ significantly when a female's nearest neighbour was in front
of her, to the left, to the right, above, or below her. Additionally, the rate of SDB in each
of these conditions did not differ from the rate of SDB that occurred when a female was
alone (no neighbours within 5 m). The only significant change in rate of SDB occurred
when a female's nearest neighbour was located behind her.

The hypothesis that arousal is reduced when the nearest neighbour is not the focus of
attention due to a lack of perceived affordances for social interaction was partially
supported: the rate of SDB when the nearest neighbour was located behind the female
was lower than when the neighbour was in any other location, however it was not similar
to her rate of SDB when she had no neighbour (as was predicted due to there being no
perceived affordances for social interaction when alone). The rate of SDB when a female
was alone did not differ from when she had a neighbour within her visual field.

An additional explanation consistent with these results is that females may only leave
their back turned to a conspecific in situations where risk of agonism is low, and

correspondingly, the need for their neighbour to be within their immediate visual field is low. Previous research has demonstrated an increase in vigilance and social monitoring during times of social uncertainty (Hirsch, 2002; Kutsukake, 2006; McNelis & Boatright-Horowitz, 1998; Watts, 1998), and this increase in vigilance would be expected to produce a reorientation of the individual's direction of attention towards the source of arousal. Support for this explanation comes from the finding that females spent significantly longer durations of time with their subordinate neighbours located behind them than their dominant neighbours, suggesting that it is of greater importance to keep dominant neighbours within their field of view. The sample of nearest neighbours would then become biased towards having subordinate neighbours located behind the focal individual, and dominant neighbours located within their visual field.

A decrease in SDB when the nearest neighbour is not visually salient (i.e., behind the focal animal) as compared to the 'alone' condition would suggest that females are, nevertheless, behaviourally influenced by group members that are not the current focus of their attention. Furthermore, although focal females were biased towards leaving their back turned to subordinates, both dominant and subordinate neighbours produced the same increase in SDB when located in the focal female's field of view. The data presented here, therefore, do not negate the social affordances hypothesis. If one takes into account the fact that, for group-living primates, being alone may induce a state of arousal due to an increase in predation risk, the finding that the rate of SDB in the 'alone' condition was similar to the rate of SDB with a nearest neighbour in any visually salient position would be easily explained. It therefore seems likely that arousal increases when

alone (due to a perceived increase in predation risk), and when the nearest neighbour is visually salient (due to perceived affordances for interaction); however, when the risk of confrontation is low, animals may leave their backs turned to their nearest neighbour, thereby reducing the rate of SDB because of the reduction in both predation risk and social affordances.

This unique approach to examining how non-human primates perceive their three-dimensional social environment places emphasis on the inclusion of emotion (as assessed through behavioural changes) in developing a comprehensive understanding of social arousal. It also demonstrates the importance of accounting for the relative spatial locations of individuals within a troop when investigating arousal in various social situations. Additionally, this study focused only on the spatial location of individuals with respect to the focal animal; however, further studies should address the question of whether perceived social affordances (and hence, degree of social arousal) differ when the neighbour is oriented towards or away from the focal animal. In summary, this research demonstrates that although proximity to certain individuals may be a valuable indicator of changes in arousal, examining details of the animals' orientation with respect to other group members provides a more all-encompassing view of social arousal by accounting for an individual's perception of the situation.

Chapter 5

IS PASSIVE OBSERVATION OF HABITUATED ANIMALS TRULY PASSIVE?

Abstract

The term 'habituated' is sometimes mistakenly used to imply that animals no longer respond to the presence of a human observer. There is an accumulating body of evidence, however, suggesting that habituated animals that no longer perceive humans as a direct threat nevertheless continue to respond to their presence in other ways. Data were collected from a troop of free-ranging vervet monkeys in the Klein Karoo of South Africa for months 5-12 of their habituation period to determine how self-directed behaviours (SDB) were influenced by human presence across time. SDB decreased across the 8 month period, indicating that habituation was ongoing. The human observer's spatial location had a significant effect on the rate of SDB, and this pattern did not arise until the later habituation period (9-12 months). Furthermore, the pattern of changes in SDB rate observed in response to the location of a human observer mimicked the pattern observed in response to a conspecific neighbour. This evidence suggests that animals continue to respond to human presence as they become habituated, although the observed responses change.

5.1 Introduction

The presence of humans is known to influence the behaviour of wild animals in a variety of ways (Jack, et al., 2008; Taylor & Knight, 2008; Walker, Boersma, & Wingfield, 2006; Webb & Blumstein, 2005) which can be classified into three response types: attraction, habituation, and avoidance (Whittaker & Knight, 1998). Much scientific research surrounding the behaviour of wild animals, particularly in the field of primatology, is based on habituation of subjects prior to the recording of observational data (Williamson & Feistner, 2003), with the goal of attaining passive observation. In other words, passive observation assumes that habituated study subjects no longer respond to the presence of the researcher, such that their natural behaviour can be recorded without the observer having any impact.

Although it is convenient to assume that observers of habituated animals are no longer influencing their behaviour, this may not be a valid assumption. Habituation is the reduction of a response to a repeated stimuli that is neither aversive nor beneficial (Bejder, Samuels, Whitehead, Finn, & Allen, 2009; Thorpe, 1963; Whittaker & Knight, 1998); however, behaviour can be influenced in ways that are not directly related to the perception of a human observer as either a threat or an attractive stimulus. For example, the presence of humans has been documented to reduce predation rate in a group of vervet monkeys in Kenya (Isbell & Young, 1993). This reduction in predation rate is thought be attributable to the differing levels of habituation between vervets and their predators (Isbell & Young, 1993), and consequently, may result in an overall reduction in vigilance/predator scanning behaviour over time due to a decrease in overall predation

risk. Natural rates of vigilance and predation may therefore not be observed in such groups, despite habituation to human presence. Such research suggests that although habituation can reduce or eliminate an animal's perception of a human as a threat, it may not be possible to completely eliminate any influence on their behaviour. Observers of habituated animals should thus take into account all of the ways in which they may influence the behaviour of their subjects, and consider whether their presence may be confounding their data in any way.

In the current study, I assessed whether the degree of arousal experienced by vervet monkeys (*Chlorocebus aethiops*) was influenced by the spatial location of the human observer (i.e. whether the observer was located to the front, back, left, or right of the focal animal) and whether any observed effect changed across time as a result of increasing habituation. The spatial location of neighbouring conspecifics has been demonstrated to influence arousal in this population of vervets (see Chapter 4), thus, it is hypothesized that vervet monkeys may also respond differentially to other animate objects (e.g., a human observer) located in each of the four regions of space surrounding the focal animal. It is expected that any changes in SDB due to the location of the observer will be independent of habituation, thereby demonstrating that truly 'passive' observation may not exist, and the presence of a human observer who is not perceived as a threat can, nevertheless, influence the behaviour of wild animals.

5.2 Methods

5.2.1 Study Site

The study site is situated in the semi-arid Klein Karoo of South Africa (32º 22`S, 24º52`E) at an altitude of 846m. With a mean annual rainfall of 330 mm, most of the surrounding area is uninhabitable by vervets apart from the woodland surrounding drainage-line riverbeds. These riverbeds only flow in times of heavy rain in their catchment area, but nonetheless contain fairly permanent pools of water throughout most of the year (c.f. McDougall, et al., 2010). The woodland surrounding the milk river, where the focal study troop resides, is dominated by acacia (*Acacia karoo*), Karee (*Rhus lancea*), and Peruvian pepper (*Schinus molle*), all of which are primary food sources.

5.2.2 Subjects

Data were collected from October 2008 to June 2009 from a single troop of free-ranging vervet monkeys. Individual identification of subjects was possible from a combination of characteristic facial features, coat color, body size, tail posture/length and scars/wounds to the face, ears, body and/or tail. Troop size was approximately 70 individuals. This included 22-24 adult and sub-adult females and 13-18 adult and sub-adult males. 13 infants were born between October and November 2008. Sub-adults were counted as those who participated in the 2009 breeding season, but in the case of females, did not yet have elongated nipples (indicative of nursing offspring), and in the case of males, were larger than adult females, but not yet adult size.

11 females in the troop were chosen as focal subjects. The entire troop received approximately 4 months of habituation time prior to the start of the study period, and data

collection from each female began once they were easily followed within 10 m and no longer showed fearful responses to being followed (e.g., they did not run from the observer or attempt to hide in trees or shrubs). A minimum of 40 hours of focal data were collected from each test female.

5.2.3 Data Collection

The monkeys were followed on foot for 10 hours per day. Daylight hours were divided into four equal time blocks and focal samples from each female were distributed evenly across the time blocks. Data were not collected from the same focal subject more than once per day in each time block. The length of each time block fluctuated between 2.5 and 3.5 hours depending on the seasonal photoperiod. Focal samples were 20 minutes in length from October 2008 through to March 2009, and were 30 minutes in length after that. A focal sample was terminated if an individual went out of sight for more than 5 minutes.

Data were collected on a Palm Tungsten^{TM} E2 Handheld using Pendragon 5.1 (2005-2007) software. An instantaneous 'scan' sample was collected at the start of every focal animal follow and every two minutes throughout. Scan samples included a record of the distance and location of the human observer (scored as < 2 m, 2-5 m, 5-10 m, or >10 m), and the ID and location of every conspecific adult/sub-adult neighbour within the focal animal's 5 m radius. Observer and conspecific locations were divided into four mutually exclusive regions of space: front, back, left, and right. These spatial locations projected in a triangular fashion away from the focal individual such that they filled the five metre

region of space around the monkey. Due to the observer being unable to manoeuvre

effectively throughout the vervets' three-dimensional habitat, only the two-dimensional

plane was examined in this investigation. Thus, data from when the focal animal was

located directly above the observer were excluded from analysis.

Self-directed behaviours (SDB) were recorded continuously during focal animal follows

according to the following categories:

1) Scratch – the fingertips of the hand or foot are drawn across the fur/skin of the body in

a repetitive motion.

2) Self-groom – examining various body parts or slowly brushing through their hair and

picking at the skin with one or both hands.

3) Body/head shake – shaking of the head and neck, sometimes followed by shaking of

the entire body.

4) Yawn – tilting the head back and gaping the mouth.

A new SDB was recorded any time an individual switched to a new class of SDB or if

there was a break of >5 seconds between bouts (for scratching and self-grooming). Each

time a SDB was scored, the distance and location of the observer and all conspecific

neighbours were recorded in the same fashion as that of the instantaneous samples.

5.2.4 Analysis

A rate of SDB was obtained for 4 different observer locations within the focal animal's 5

m radius (front, back, left, and right). This was done by dividing the total number of

SDB that occurred when only the human observer was located in each of the spatial

locations (i.e., no conspecific neighbours within 5 m), by the total amount of time spent in the corresponding condition (for example, under condition x: SDB_x/(scan samples$_x$*2).

The side condition (i.e. when the human observer was <5 m to the left or right of the focal female) was divided into its corresponding left and right components and compared using the Wilcoxon signed ranks test. The rates of SDB for each spatial location of the observer (front, back, and side) were then compared using Friedman's repeated measures ANOVA. Post hoc analyses for pairwise comparisons were performed using Wilcoxon signed ranks tests with an applied Bonferroni correction.

Spearman's correlation was used to examine whether changes in the rate of SDB due to a human observer being present in a particular spatial location were similar to changes observed when a conspecific was present in the same spatial location (Chapter 4).

Finally, an investigation into whether an increasing degree of habituation would result in a decreasing response to human presence was conducted. This analysis included a temporal comparison of SDB rates across the 8 month data collection period, when only the human observer was within 5 m of the focal animal. A linear regression determined whether SDB rates declined or remained stable during this time. Next, the study period was divided into four month periods and Friedman's ANOVA was used to test whether observer location had an effect on the rate of SDB in both the first and second periods. Additionally, the change in rate of SDB between the first and second period was compared for each observer location using the Wilcoxon signed ranks test.

5.3 Results

The mean (± SEM) rate of SDB for each of the four observer locations is given in Table 5. A comparison of the two components of the side condition (observer located on the left or right) indicated that the rate of SDB did not differ between these two conditions (Wilcoxon signed ranks test: z= 0.178, p=0.859), therefore these data were pooled into the 'side' location for further analyses.

Observer location had a significant effect on rate of SDB (Friedman's ANOVA: $X^2(2)$=6.186, p=0.045). Post-hoc pairwise comparisons indicated that rate of SDB was significantly lower when the observer was located behind the focal animal than when located to the front or side (behind vs. front: z=2.402, p=0.048; behind vs. side: z=2.578, p=0.030) The rate of SDB did not differ when the observer was located to the front or side of the focal female (front vs. side: z=1.990, p=0.141).

The rate of SDB when a human observer was located behind or to the side of the focal animal was significantly correlated with the rate of SDB observed when a conspecific neighbour was present in the corresponding location (Table 6).

Table 5. Mean ± SEM rate of self-directed behaviour (SDB) for the 11 focal

females when a human observer was located in each of the four locations.

Observer location	Mean Rate of SDB	SEM
Front	0.37	0.03
Back	0.24	0.03
Left	0.31	0.09
Right	0.31	0.09

Table 6. Correlation between the rate of SDB expressed in response to a conspecific and a human observer located to the front, side, or back of the focal animal. Shaded boxes indicate correlations significant at the p<0.05 level.

Spearman's Rho Correlation Analysis

		Observer location		
		Front	Side	Back
Front	Correlation Coefficient (r)	0.445	0.364	0.491
	Sig. (2-tailed)	0.170	0.272	0.125
Side	Correlation Coefficient (r)	0.373	0.791	0.845
	Sig. (2-tailed)	0.259	0.004	0.001
Back	Correlation Coefficient (r)	0.445	0.591	0.691
	Sig. (2-tailed)	0.170	0.056	0.019

* Data for conspecific location from McDougall, submitted.

A linear regression indicated that the rate of SDB decreased across the duration of the study (r^2=0.082, B= -0.012, β= -.287, p=0.007) (Figure 7). The data collection period was therefore divided into two four month periods for further analysis. The rate of SDB was not found to differ between conditions in the first four month period (Friedman's ANOVA: X^2(2)=5.091, p=0.078), whereas observer location had a significant effect on the rate of SDB in the second four month period (X^2(2)=13.636, p=0.001). Post-hoc analysis showed, once again, that the difference was between the behind condition and both the front and side conditions (behind vs. side: z=2.937, p=0.009; behind vs. front: z=2.758, p=0.018), while the latter two conditions did not differ (z=1.336, p=0.543). This pattern is the same as that observed in response to conspecific neighbours (Chapter 4)(Figure 8). Rates of SDB when the observer was located to the front or side of the focal animal did not differ between the first and second data collection periods (front: z=0.178, p=0.859; side: z=0.816, p=0.414); however, the rate of SDB when the observer was located behind the focal animal decreased significantly in the second data collection period (z=2.936, p=0.003)(Figure 9).

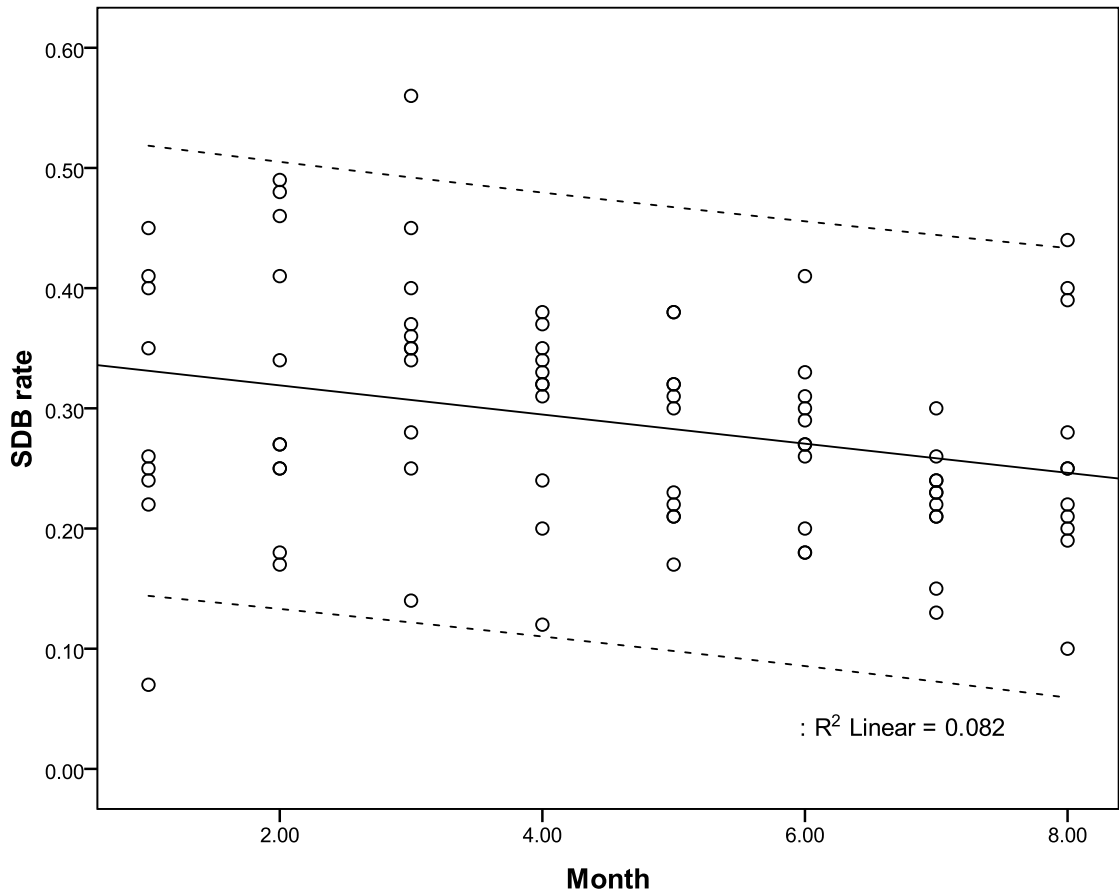Figure 7. Open circles indicate the mean monthly rate of SDB for each of the 11

focal animals when only the observer was present within their 5 m radius. A

linear regression indicated that duration of habituation time (month) explained 8%

of the variation in rate of SDB across time, with an average monthly decrease of

0.01 SDB/min (solid line). Dotted lines indicate the 95% confidence interval.

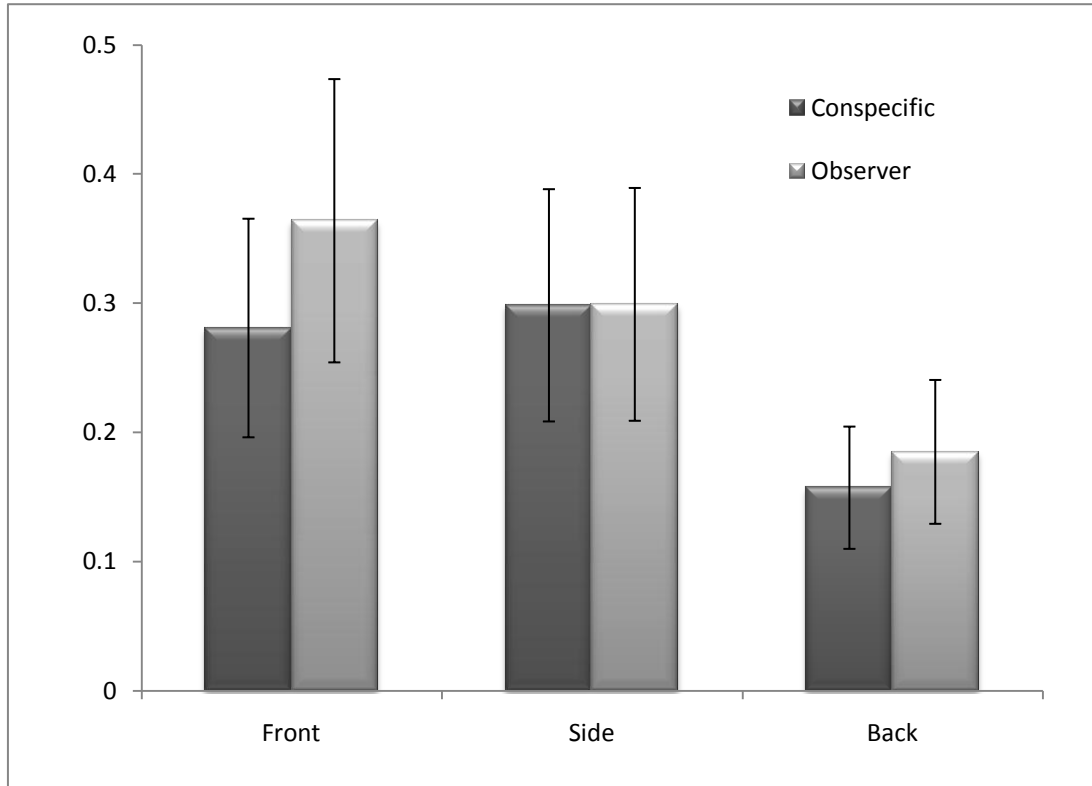Figure 8. Mean (± SEM) rate of SDB for the 11 focal animals when a conspecific or human observer was located in the 5 m region of space to the front, side, or back of the focal individual. Data for conspecific effects is reproduced from McDougall, submitted. For both the conspecific neighbours and the human neighbour, the rate of SDB was significantly lower in the back condition than the front or side conditions.
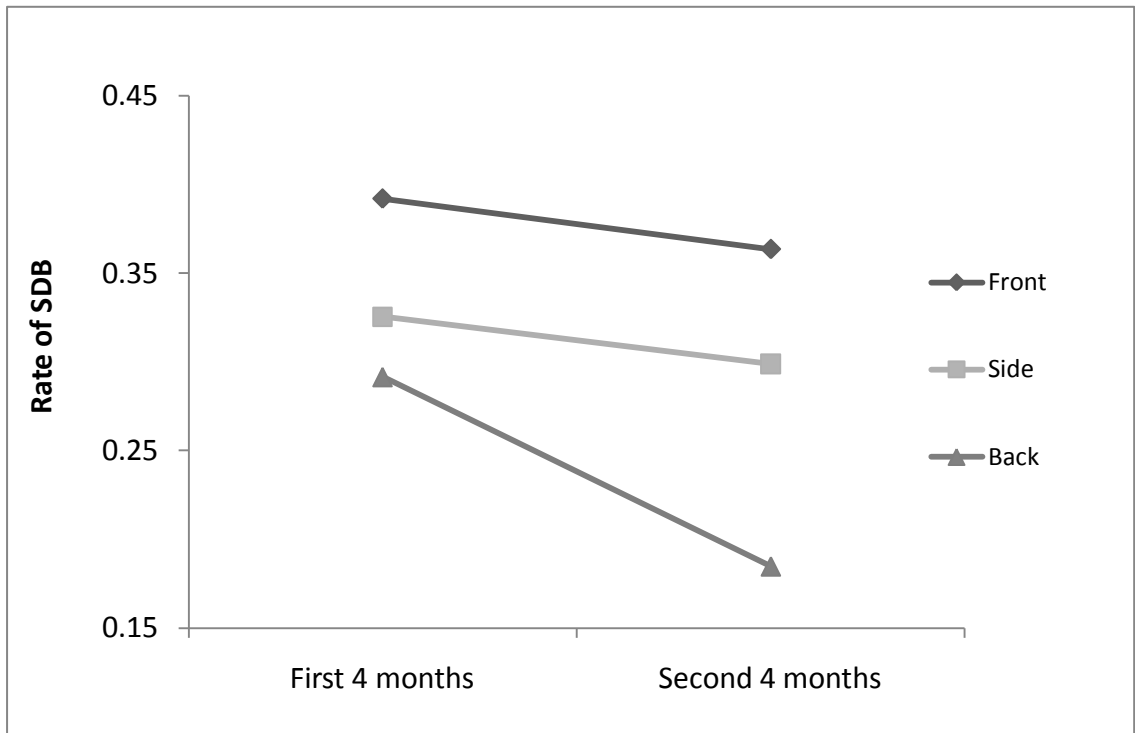
Figure 9. Comparison of the rate of SDB in the first and second habituation periods for each of the human observer's spatial locations. The front and side conditions showed a non-significant declining trend in rate of SDB. The back condition indicated a significantly reduced rate of SDB in the second data collection period (corresponding to months 9-12 of habituation).

5.4 Disscussion

Observer location had a significant effect on a vervet monkey's rate of SDB. SDB rates were lower when the observer was located behind the focal animal, whereas no other locations differed. This pattern was similar to the pattern observed in response to conspecific location. The focal subjects showed a decrease in their rate of SDB across the duration of the study period, suggesting that habituation was ongoing. Furthermore, when the data collection period was divided into an early and late phase, the pattern of decreased SDB when the observer was located behind the focal animal was not evident until the later phase, suggesting that the pattern may be related to the vervets' changing perception of a human observer during the habituation period.

The overall rate of SDB when only the observer was present in the focal animals' 5 m radius decreased over the 8 months of data collection. Thus, although the four months of habituation prior to the start of data collection brought large scale behavioural changes in the monkeys (e.g. no longer threatening, running from, or hiding from human observers), continued habituation was evident from small behavioural changes (i.e., SDB) for at least a year, though at a much slower rate (SDB rates decreased by only 0.01 per month in the 8 month data collection period and the 'time' variable explained very little of the variation in SDB rates). Jack et al. (2008) also noted evidence of continued habituation in the form of decreasing cortisol levels from a group of capuchins in Costa Rica following the conclusion of an 18 month behavioural study. Therefore, although large scale behavioural changes may occur fairly quickly, less overtly noticeable indicators of habituation (e.g., cortisol, SDB) may decrease over a much longer period than previously

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estimated (Williamson & Feistner, 2003).

Dividing the study period into the early and late phases of habituation revealed an interesting effect: specifically, that differences in rate of SDB resulting from the observer's spatial location did not become evident until the late phase of habituation (i.e., months 9-12). Furthermore, the pattern that emerged at this time mimicked the pattern observed in response to conspecific neighbours (Chapter 4). This finding suggests that particular behavioural responses to human observers may only appear once animals are sufficiently habituated and no longer perceive humans as a potential predator or threat. Other non-predator species such as buffalo (*Syncerus caffer*) and kudu (*Tragelaphus strepsiceros*) also regularly forage alongside the vervets in this region, although whether the vervets also respond to these animals in a similar manner to human observers has yet to be determined. If this is the case, non-threatening animate beings should not be considered neutral stimuli, as all living animals that occupy the same area as the species under investigation have the potential to produce positive and negative effects. For example, Rasmussen (1991) found that the ranging patterns of stumptail macaques (*Macaca arctoides*) were still influenced by human presence after 14 years of observation. Similarly, chimpanzees (*Pan troglodytes*) and capuchins (*Cebus capucinus*) showed observer-directed behaviours such as threats, play solicitation, watching, and throwing objects at observers after being habituated for up to 24 years (Jack, et al., 2008; Nishida, et al., 2009). Domestic livestock also respond to direct gaze from human observers by watching them more frequently, but show no increase in fear-related behaviours, thereby demonstrating that although human observers do not represent a

direct threat, altered behavioural patterns are still evident (Beausoleil, et al., 2006). The term 'habituation' may therefore be better suited to imply that animals will no longer perceive humans as a direct threat, rather than indicating that animals no longer respond to our presence (Knight, 2009). This is an important distinction, as it may not be possible to ever completely ignore the presence of another animate being moving amongst a group, and moreover, some human induced behavioural responses may only appear once the individuals reach a certain level of habituation. Researchers should therefore be cautious about what they are implying when stating that their animals were habituated to human presence and consideration should be given to all of the ways that behaviour may be influenced by observation in close proximity.

6.0 Comprehensive Discussion

The research presented in this thesis suggests that self-directed behaviours are an effective, non-invasive and easily observable behavioural indicator of arousal that can be used to gain a comprehensive understanding of how monkeys perceive various social situations. The first research chapter indicated that rate of SDB was influenced to a greater extent by the degree of association between individuals than by dominance rank. It is not clear why this effect was found, but it appears that differing rates of aggression may still play a role in changes in arousal related to association. Furthermore, predictability of behaviour might also be influencing social arousal and it is possible that these two variables interact in a way that renders them inseparable. For example, it could be hypothesized that increased predictability of behaviour in associates may be sufficient in preventing outbreaks of aggression (e.g., associates may express their intent in more subtle ways due to their greater degree of experience with each other, and these may be more difficult for a human observer to pick up on). Moreover, in non-linguistic species, what appears to be agonistic behaviour to a human observer may not be perceived in the same manner by animals whose only means of mediating social space, and other needs, is communicating through body language. If you can't *tell* someone that you feel uncomfortable with them being too close, you need to communicate your needs in another way, and for vervet monkeys, a brief eyebrow raise may accomplish this nicely. This interaction between subtlety of body language and greater experience with associates' behaviour might be responsible for producing the apparent increase in number of agonistic interactions per unit time among dominant non-associates. Thus, the results of this study indicate that association is an important variable that has often been

overlooked, and further research into the effects of association on social arousal are needed.

In addition to examining the effects of dominance and association, my research examined how a third variable - the spatial location of a nearest neighbour - influenced the level of arousal an individual experienced. The nearest neighbour's location was documented with respect to the focal animal's body orientation, thus allowing for more precise investigation into conditions of social arousal by accounting for the fact that an individual is not likely attentive towards a nearest neighbour located behind them. Arousal inducing stimuli, such as potential social partners, that are not the focus of an animal's attention are not expect to influence behaviour to the same extent as social partners that are in a prime location to be perceived. This effect was also used to investigate how the presence of a human observer influenced the behaviour of free-ranging monkeys as they became habituated. The same pattern of changes in arousal due to the spatial location of a conspecific was found in response to a human observer. Interestingly, however, this effect did not appear until the later stages of habituation (months 9-12), suggesting that perception of a human observer as a non-threatening social stimulus may be a necessary requirement for this response to be observed. More importantly, it indicates that animals may still respond to the presence of a human observer despite prior habituation. Rather than *reducing* the effects of human presence on the behaviour of wild animals, habituation may instead be *altering* the observed effects. SDB therefore appears to be a reliable indicator of how vervet monkeys perceive their social world in terms of both intraspecific and interspecific effects.

As was noted in the introduction, the lack of discrimination between positive and negative emotional valence is something that has not been determined for many indicators of emotion, including self-directed behaviours (Boissy et al., 2007). Accordingly, the main limitation of this study is the difficulty of interpreting an individual's perception of a social situation using an ambiguous measure of emotional valence. Determining emotional valence may prove to be a difficult task, as many physiological indicators of both positive and negative emotion function similarly to prepare the animal for action. Neuroendocrine evidence indicates that activation of the 'stress axes' (the adrenocortical axis and the autonomic nervous system) correlates with both positive and negative emotional activation (Boissy, et al., 2007), thereby further highlighting the inappropriateness of equating the term 'stress' with negative affect. The word 'stress' arose ca. 1300 from the Latin term 'strictus', meaning 'compressed', and modern biological psychology textbooks often define stress as "the non-specific response of the body to any demand made upon it" (Selye, 1979). These definitions highlight not only the difficulty in interpreting a stressful or arousing situation as positive or negative, but more to the point, that positive and negative emotions may not be distinguishable purely from measures of intensity. In fact, as you may recall from the discussion of approach-withdrawal conflict in the introduction, high emotional intensity, by its very nature, may often be produced by adding both measures of valence to a single situation. If it is primarily uncertainty that produces increases in arousal, then situations that are exclusively positive or exclusively negative may not invoke an element of uncertainty or conflict in decision making, and as such, would not be expected to result in such large increases in emotional intensity. Although this discussion of intensity vs. valence

suggests a limitation to studies of SDB, and emotional arousal more generally, it is not necessarily a limitation of non-human 'animal' studies in emotion, but rather a limitation of the working definition of emotion and of the meanings implied by current terminology in the literature.

According to Demasio (1999), emotions can be distinguished from feelings in that emotions consist of overtly measurable behaviours, whereas feelings are the conscious experience of the emotion. The James-Lang theory of emotion suggests that this 'conscious feeling' is produced by reflecting on our behaviour and that this reflection subsequently provides us with a means of labelling our emotions (James, 1884). For example, we might see a bear suddenly step out of the woods in front of us and our immediate behavioural response is to scream and run in the opposite direction. The act of screaming and running then causes us to infer the feeling of fear. Although the James-Lang theory describes the emotion as the label given to the feeling or experience, it still places a distinction between behaviour and the conscious experience that we use to label the event. The fact that the terminology and definitions used by Demasio and James-Lang differ further emphasizes the need to standardize the use of terms to avoid confusion and disagreement between studies. Furthermore, the James-Lang theory argues that physiological arousal is both necessary and sufficient for emotion because the conscious experience and subsequent label that we give the emotion is only our perception of the response (Kalat, 2004). This theory implies a very unidirectional model of emotion (behaviour produces feeling) that is somewhat counterintuitive to a layperson's model of emotion, in that one would generally be inclined to think the

reverse, *i.e.* that feelings produce behaviour (concordant with the original Latin term 'emovere' which suggests that behaviour is a reflection of an internal psychological state, or 'feeling'). In fact, it is likely that both of these theories are true. In using Bradley & Lang's (2000) three components of emotion (behaviour, physiology, and feeling) one could argue that there is bidirectional influence of each component on the other two in the system, and that together they comprise an emotion.

Although emotions may include three different elements with bidirectional influence on each other, this still leaves the question of where the labels for various emotions come from. The James-Lang theory suggests that the label assigned to an emotion is based on perception of our body's response; however, these labels can often be wrong. In a classic study by Dutton and Aron (1974), males that encountered an attractive woman while on a suspension bridge reported that they were more strongly attracted to her than males who were not in a situation of high arousal. They proposed 'misattribution theory' to explain their results by arguing that ambiguous arousal caused by one situation may accidentally be attributed to another non-related situation. In other words, they suggested that the males were more attracted to the woman because they mistakenly attributed their heightened arousal to feelings of attraction for her rather than to the fact that they were suspended 450 ft above a deep canyon. Accordingly, scientists may infer positive or negative arousal based on the current social scenario, but if humans have been shown to mislabel the cause of their own arousal, what gives us the authority to assign a cause for an animal's increase in arousal. In other words, changes in rate of SDB tell us only about which situations are arousing, but imply nothing about why. For example, increased

arousal in the presence of a particular social partner may indeed be due to an increased risk of aggression, but alternatively, it may be due to the presence of a frequent play partner, or a relative that hasn't been seen for awhile. Elephants, domestic dogs, and many other animals, often show signs of increased arousal and high energy behaviours when greeting relatives or other familiar social partners that have been absent for a period of time (personal observation). Future studies should aim to verify whether SDB is a response to the general intensity of the emotion or whether it correlates with a particular type of affect. The current body of literature on SDB is heavily based on correlations with situations of apparent negative affect, and this appears to have severely biased not only our interpretations of changes in arousal, but also narrowed the tunnel through which new research is focused. We need to take a step back and question exactly what is being measured before adding layers of complexity involving such things as emotional valence to this type of research.

Reefmann and colleagues (2009) recently attempted to determine if several physiological and behavioural measures were correlated with positive or negative emotion in domestic sheep. Their findings, however, appeared confounded by emotional intensity (i.e., arousal), such that their test for negative valence (separation from group members) increased arousal and their test for positive valence (receiving grooming from a familiar human) decreased arousal. In other words, testing for positive or negative physiological indicators of emotion would require four test scenarios: positive and negative arousal reducing situations as well as both positive and negative arousal inducing situations. Spruijt et al., (1992) suggested that grooming is involved in the arousal reduction process,

and although the decline in arousal that accompanies grooming may be positive, there exist other situations in which low levels of arousal may induce negative affect. For example, boredom and depression are associated with a reduction in arousal (Posner, Russell & Peterson, 2005) and would therefore be hypothesized to produce the same behavioural and physiological changes as grooming despite their negative emotional valence. Studies investigating behavioural and physiological correlates of emotional valence would thus benefit from examining differences between positive and negative situations that evoke a similar degree of arousal. Similarly, we should question our tendency to link only negative affect with negative long-term consequences. It may be that the negative effects associated with glucocorticoid release (*i.e.* chronic arousal), such as immune suppression and impaired reproduction (Sapolsky, 2005) are not specific to prolonged periods of negative arousal, but rather to the non-specific maintenance of above-optimal levels of arousal, regardless whether positive or negative.

In his book 'Blink', popular science writer Malcolm Gladwell (2005) discusses how our behaviour changes with our current level of arousal. An optimal level of arousal (*e.g.* a heartbeat between approximately 115 and 145 beats per minute) is said to improve performance, whereas above-optimal levels of arousal cause blood to be drawn away from the outer muscle layer and concentrated in essential physiological activity. This change in blood flow and physiological activity reduces cognitive functioning, fine motor ability, and a suite of other processes. These effects are evident whether above-optimal levels of arousal are produced from apparently positive (*e.g.* sporting events) or negative (*e.g.* crimes involving weapons) situations. Therefore extended periods of positive

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hyper-arousal may also lead to undesirable consequences.

With respect to self-directed behaviour, there are several indications that these displacement activities increase in frequency with positive, as well as negative, emotional arousal. For example, the rate of SDB increases in the period surrounding a bout of allogrooming (personal observation; Manson & Perry, 2000); a presumably positive social experience, whereas negative social interactions such as chasing and biting also produce an increase in SDB (Maestripieri, et al., 1992). According to the circumplex model of affect, any particular emotion can be placed on a two dimensional plot according to its level of arousal and valence (Russell, 1980; Posner, et al., 2005). It therefore follows that at least two indicators of affective state should be used (including at least one measure of valence and one of arousal) in order to more accurately determine the emotions involved. The research and accompanying literature presented here suggests that SDB rate is indicative of only emotional intensity (*i.e*., arousal) and a second emotional measure related to valence is therefore recommended to accompany SDB research such that a more complete view of an animal's social perceptual world can be obtained. The problem, however, with experiments designed to investigate emotional valence is that we once again return to the problem of anthropomorphism. Any test designed to invoke negative affect, with the goal of finding physiological and behavioural correlates, will be designed from a human perspective. In fact, 'feeling' may be the only one of Bradley and Lang's (2000) three emotional components that can distinguish between positive and negative emotional valence, thus, non-human animal studies that investigate the behavioural and physiological components of emotions may only provide

data along the arousal axis, with no regard for the valence axis in the circumplex model of emotion. Whether scientists can truly understand emotion in non-human animals without the valence or 'feeling' component (or even whether humans can interpret their own feelings correctly) is open for debate. In the meantime, however, it is important for researchers to remain aware of limitations to interpretation of behavioural and physiological data, and to avoid confusion between arousal and valence when investigating emotional states in animals.

In addition to distinguishing between valence and arousal in drawing a picture of an animal's socio-perceptual world, one must also recognize the importance of attention. Stimuli that are not the current focus of attention are not likely to have the same effect on the emotional state of an animal as stimuli that an animal is attentive to. Attending to an object or event thus provides 'affordances' to an individual in terms of perceived opportunities and possibilities for action (Chapter four provides a discussion of affordances as they relate to attention and social interaction). As humans, we emphasize the importance of eye gaze in determining an individual's direction of attention, however, this may be problematic for animals whose primary sensory modality is tactile, olfactory, or auditory, rather than visual (Bushnell, 1998). Additionally, it is thought that the high degree of contrast between the dark iris/pupil and the white sclera in humans has lead to greater efficiency in the ability to follow eye gaze (Emery, 2000). Head and body orientation may, therefore, be a better proxy for general direction of attention in non-human animals. Because much of social arousal likely depends on the probability of interaction between two individuals, future studies examining not only the orientation of

the focal animal, but also the direction of attention of the nearest neighbour may be beneficial. In fact, it is possible that changes in a focal animal's rate of SDB may influence their neighbour's behaviour in terms of communicating their level of arousal (provided that the neighbour is attending to the focal animal). Note that I am not implying any kind of intentionality in using the term communication here; rather, that overt behaviours may cue other attentive individuals to act in a particular manner. For example, a dominant individual seeking a space in a good quality foraging patch may pick out a highly aroused subordinate as an easy target for displacement. Although in this case increased SDB may place the animal at a disadvantage, there are situations where a benefit may be had from overt displays of arousal. If emotional contagion causes an attentive neighbour to also become highly aroused, the two individuals may engage in a bout of allogrooming, thereby providing the mutual benefit of decreasing arousal. These examples of how social interactions may be influenced by observing overt indicators of arousal suggest that SDB may have multiple functions.

This finding thus brings into question the definition of self-directed behaviour, or so-called 'displacement activities'. As stated in the introduction, self-directed behaviours are displacement activities that do not appear to be related to their everyday purpose, *e.g.,* scratching in situations of high arousal does not appear to be for the purpose of satisfying an itch. However, if SDB serves the purpose of mediating social interactions, or effectively reducing arousal to an optimal level, then these functionally adaptive explanations for scratching behaviour are just as valid as scratching to satisfy an itch. The line between what is displacement behaviour and what is behaviour being performed

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in its 'original context' therefore becomes blurred. If the behaviours produced in each context are similar in nature, then it may be impossible to determine which function they are currently serving. Although this suggests the need for a new definition of displacement behaviours, it also does not affect the results of studies involving measurement of these behaviours as long as scientists acknowledge that a baseline rate of SDB likely serves various functions and that it is the *change* in rate of SDB that is correlated with particular social scenarios that is of interest. Furthermore, if displacement activities function to reduce an individual's level of arousal, then this definition may include a far wider range of behaviours than the average study of arousal includes. Indeed, as arousal increases, the overall general activity level of an animal likely increases as well. For example, frequency of ear posture changes have been shown to correlate with increased arousal in sheep (Reefmann *et al.,* 2009). Therefore, we should use a definition of displacement activities that accounts for the multiple functions they serve rather than attempting to define them by the function that they are not currently serving.

In summary, the research presented here added to the literature exploring social influences on arousal, however, in attempting to interpret the findings presented in this thesis, a large unexplained bias towards interpreting arousal as a negative experience was found to exist within the literature. Following with this bias, displacement activities also appear to be used almost exclusively to investigate negative social situations without regard for the fact that there is no evidence suggesting that SDB reflects only changes in negative arousal. Thus, although the research itself is likely valid, it is entirely possible

that interpretations of the data are wrong and dangerously misleading. To make progress in the field of animal and human emotions, we must first investigate what exactly the behaviours in question are measuring. This requires going back to the drawing board and creating carefully controlled experiments (*e.g.* when displacement activities are demonstrated to correlate with negative arousal, we need to test whether they also correlate with positive arousal before drawing any conclusions). In taking a step backwards, scientists will hopefully be able to get out of the narrow tunnel that is currently guiding research on SDB and anxiety, and approach the subject from a fresh, broad perspective. Although this finding suggests a limitation to this type of research, provided this limitation is acknowledged, it should still prove to be valuable in combination with other forms of data on emotion. It is hoped that exposing this bias will spark new avenues of research to come to light within the discipline of emotional arousal.

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APPENDIX

8.1 Comparison of proximity association networks and grooming association networks*

Patterns of association were recalculated using the grooming data from the 11 female focals. The repeated measures ANOVA produced a significant result for the model (F=5.690, df=2, p=0.014), and pairwise comparisons indicated that the difference was also between the dominant non-associates and the other two classes (dominant associates & subordinate associates), but not between the latter two classes (Figure 10). This result was not as robust, as it did not withstand a conservative alpha level adjustment for multiple comparisons (the Bonferonni), but it remained significant with a very liberal multiple comparison procedure (the least significant difference, or LSD) (Tables 7a & 7b).

The main problem associated with presenting this data is that the scan samples used to determine the grooming index could not be considered independent because they were done every two minutes throughout the focal and grooming bouts lasted much longer than two minutes. Although the data set is large (~ 40 hours per subject), this corresponds to roughly 8-12 focals per subject. If a particular dyad was captured in a grooming bout for an entire focal, this would have a profound effect on that dyad's grooming index. More importantly, it would be impossible to obtain an accurate picture of all of an individual's grooming partners in only 8-12 focals (thus many grooming partners would, by chance, end up with a grooming index of zero). These points are reflected more clearly when comparing the distribution of the grooming index scores and the proximity index scores (note the dramatic change in the scale used on the y-axis: Figures 11a & 11b). If a grooming index were to be used for this type of study, the scan samples within the focal would need to be temporally separated by a length of time greater than the average grooming bout (half hour would be advisable), and, although it would be an interesting possibility for a future study, this is not something I have data for at present.

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* The following discussion represents a portion of a reply to a manuscript reviewer regarding an inquiry as to why I had chosen not to present the grooming data together with the association data (as Silk (2006a) did to obtain her composite sociality index). The information provided in this section demonstrates that I am not attempting to conceal anything by failing to including data on grooming relationships, as the results from the grooming index indicate the same trend as that produced from the association index. Furthermore, the data collection protocol that I used was not conducive to this type of analysis and would have imposed many problems on the dataset. I therefore chose to present only the association sociality index within chapter 3.
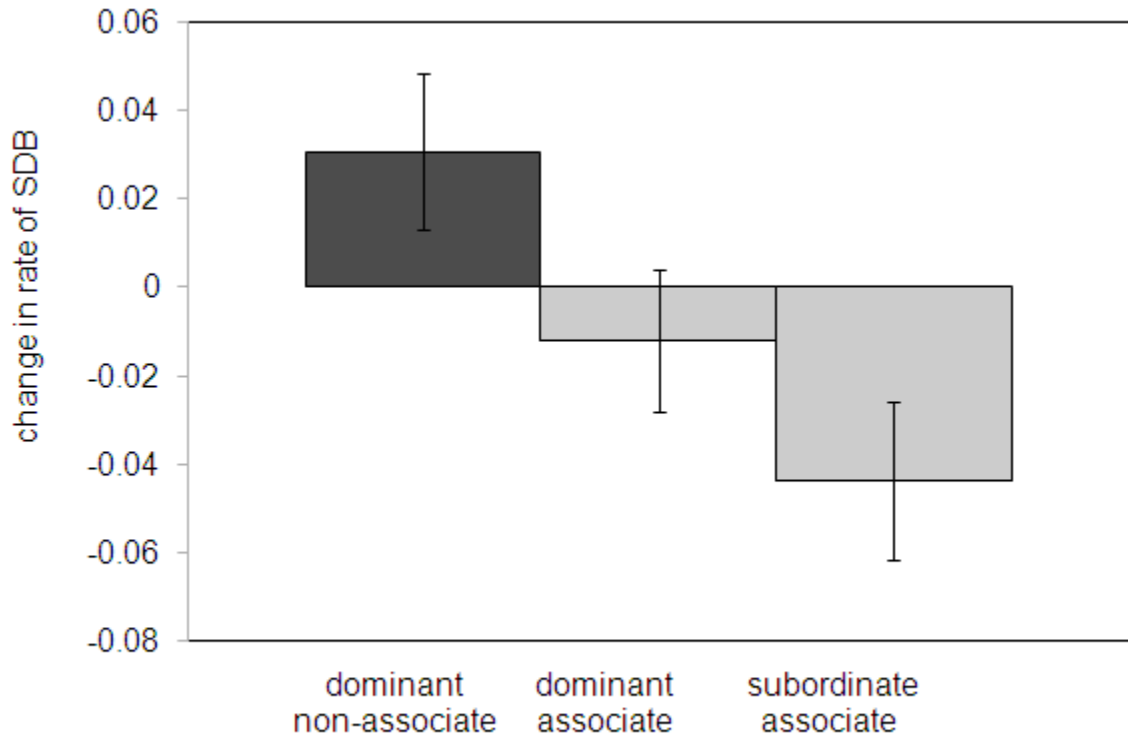
Figure 10. Change in rate of SDB when the grooming index was used to determine association class. The dark bar (dominant non-associate neighbours) differs significantly from the other two classes, but the latter two do not differ. This is the same pattern as represented by the proximity sociality index (figure 3).

Tables 7a & 7b. Repeated-measures ANOVA pairwise comparisons for grooming data

(I) neighbour	(J) neighbour	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
1	2	.050	.021	.126	-.012	.112
	3	.082	.031	.090	-.012	.176
2	1	-.050	.021	.126	-.112	.012
	3	.032	.020	.444	-.028	.093
3	1	-.082	.031	.090	-.176	.012
	2	-.032	.020	.444	-.093	.028

Based on estimated marginal means

a. Adjustment for multiple comparisons: Bonferroni.

1 = dominant non-associates, 2 = dominant associates, 3 = subordinate associates.

Pairwise comparisons using the LSD correction instead of the Bonferroni

(I) neighbour	(J) neighbour	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
1	2	.050[*]	.021	.042	.002	.098
	3	.082[*]	.031	.030	.010	.154
2	1	-.050[*]	.021	.042	-.098	-.002
	3	.032	.020	.148	-.014	.079
3	1	-.082[*]	.031	.030	-.154	-.010
	2	-.032	.020	.148	-.079	.014

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Least Significant Difference (LSD).

Numbers represent the same classifications as the previous table.

Figures 11a & 11b. Distribution of grooming sociality index scores (11a) in comparison to the distribution of proximity sociality index scores (11b). Note the difference in scale used on the y-axis.