MALE-MALE SOCIAL INTERACTIONS IN VERVET MONKEYS: TARGETS AND TACTICS

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ABSTRACT

This thesis offers an alternative to the conventional 'social intelligence' hypothesis: that the complexity of primate group emerges from dynamic, short term variation in partner availability and quality and that primate social cognition is geared to producing flexible responses to unpredictable contingencies. Using the theoretical framework that views cognition as being both 'embodied' and 'embedded' in the environment, agonistic interactions were examined with the aim to better explain complex signalling behaviour in male vervet monkeys. Firstly, agonistic interactions with and without physical aggression were examined to assess the targets of male vervets during combat. The tactics employed by the partner, such as adjusting posture and relative orientation to partner, were also investigated. This thesis also examines the influence of proximity on male behavior during agonistic interactions and interactions containing threats. Lastly, threat displays were investigated further in order to test for evidence of them occurring in a ritualized manner.

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CHAPTER ONE:
THEORETICAL BACKGROUND

1.1. Introduction:

Primate social life is considered to be particularly complex relative to that of other mammals (Humphrey, 1976; Dunbar, 1998). For cercopithecine monkeys, groups are composed of different generations, and animals experience a constant flux of births and deaths, along with immigration and emigration by adult males (see e.g., Henzi and Barrett, 2007; Campbell, Fuentes, MacKinnon, Bearder & Stumpf, 2006 for review). In addition, fluctuations in ecological conditions can also influence patterns of social interaction by altering food availability and influencing factors like group spread and competition (e.g., Barrett et al., 2003), which in turn can lead to differences in the nature of social engagement. This inherently dynamic structure and its associated unpredictability, combined with the fact that animals that lived in groups are forced into competition with each other, are thought to have shaped the size and structure of the brain and the particular ways in primates might think about the world (e.g., Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988). More specifically, it has been suggested that sociality has selected for abstract, conceptual knowledge and an ability to recognize and anticipate future events (e.g., Humphrey, 1976; Dunbar, 1998; Bergman, Beehner, Cheney & Seyfarth, 2003).

There is, however, no unequivocal evidence to show that monkeys possess either the abstract, conceptual knowledge, nor the ability to recognize and anticipate their future needs, that is assumed to underpin this 'social intelligence' hypothesis (see Barrett, Henzi

& Rendall (2007) for a critique of this position). An alternative hypothesis is that the complexity of primate groups emerges from dynamic, short-term variation in partner availability and quality and that primate social cognition is geared to producing flexible responses to unpredictable contingencies that will occur inevitably among long-lived social animals (Barrett et al., 2007). The theoretical basis for this view is that cognition should be viewed as both 'embodied', with knowledge fundamentally tied to physical acts, and 'embedded' or 'situated' in the environment (Clark, 1997; Griffiths & Scarantino, 2005). In this thesis, I investigate the social interactions of male vervet monkeys during the breeding season using this embodied and situated framework. More specifically, I investigate male-male agonistic interactions, including both physical confrontations and threat displays, in order to identify the body targets of male aggression; the tactics males use in fights; how proximity influences the use of threats and whether such interactions are ritualized or inherently unpredictable. In so doing, I consider the signal value of male threat displays and whether these represent the communication of resource-holding potential (RHP) or whether such signalling is only apparent, and represents male attempts to achieve a combat advantage over opponents (such that particular postures may serve as cues, but are not signals in a formal sense: Saleh, Alan, Bryning & Chittka, 2007)

1.2. Signaling behaviour

The embodied, embedded framework in which I situate my work contrasts with the standard view of signalling which tends to use a 'conduit' metaphor, and assumes that information is encoded by the signaller and decoded by the receiver in a manner that is uninfluenced either by environmental contingencies or the emotional state of either animal. That is, although emotional state and the state of the environment might have an influence on the production of a signal or the likelihood of responding, they do not change the 'message' contained in the signal. This is captured in one of the standard definitions used in the signalling literature: a signal is a "packet of energy or matter generated by a display or action of one organism (the signaller) that is selected for its effects in influencing the probability pattern of behaviour of another organism (the receiver) via its sensory nervous system in a fashion that is adaptive either to one or both parties" (Hebets & Papaj, 2005). Rendall, Owren & Ryan, 2009 question the conduit approach inherent in such definitions, and have suggested replacing the term "receiver" with "perceiver", which better captures what they term the "functional asymmetries" that exist between signallers and perceivers; that is, the way in which signallers and perceivers can sit at different points in an evolutionary dynamic, and may not be equally vested in the accurate transfer of information. In other words, the signals that animals use may be designed to influence the perceiver's nervous system in direct ways that may not always be in the perceivers' interests and, when they are, the details of signal design will not be arbitrary, as they are in language, but will be of central importance to the outcome of perceiving a call (Rendall et al., 2009). Alarm calls, for example, tend to share a common plosive quality that causes a startle effect in perceivers (which increases arousal and alertness), and is an acoustic feature that renders calls much more similar to each other than would be expected if they shared the language-like property of arbitrariness (and where one would predict such calls should diverge acoustically from each other as far as possible to avoid possible confusion: Rendall et al., 2009). In this study, I apply similar reasoning to visual displays, viewing these as a means by which animals attempt to influence and manage each other's behaviour rather than as attempts to inform them about some overt intention or decision to act (Owings & Morton, 1998).

Signallers often use multiple modalities to signal, and multiple signals may also be produced via the same modality (Hebets & Papaj, 2005). There have been various hypotheses put forward to explain the function of such "complex signals". There is strong support for the "multiple messages" hypothesis, which, in the standard information formulation, suggests that multiple 'packets' of information are sent within the same signal. This packet can contain information regarding dominance, RHP, fitness, species recognition or location, and different aspects can be directed at different audiences. For example, the bright coloration of vervet male scrota has been hypothesized to signal dominance RHP to other males, as well as male RHP and genetic quality to females (Gerald & McGuire, 2007; Gerald, Ayala, Ruíz-Lambides, Waitt & Weiss, 2010; Henzi, 1985). Redundancy, or the sending of different signals with the same message, is also an element of complex signalling. Redundancy can be illustrated via the "red white and blue" genital display of the male vervet, which involves indicating as aspects of RHP through the coloration of genitalia, and specific body movements/ postures adopted by the individuals engaging in the interaction (Struhsaker, 1967b).

Other hypotheses to explain complex signalling include the idea that multiple signals can act as "back ups" for each other (which obviously relates to redundancy, i.e., if one signal fails there are others that can compensate), or can be viewed as components of a larger complex signal, with one element designed to enhance the others, allowing for more efficient, improved responses. That is, signals may amplify, alter, filter, or create a context for concurrent signals (Hebets &Papaj, 2005). For example, bowerbirds commonly entice their mates by drawing their attention to brightly coloured ornaments in their bower. Once lured, the female places herself in the correct context for increased exposure to the male's other signals and thus increases signalling efficiency for the male (Borgia, 1985). It is easy to see how this can also explain the red, white and blue (RWB) displayed by male vervets, where particular postures help amplify the impact of bright genital coloration. As should be apparent, the idea that signals reflect an attempt to manage the behaviour of another individual, and that contextual variables have a great influence on signal 'meaning', can be allied to the conceptual framework of complex signalling, without any need to commit to the conduit metaphor of transmitted information, nor to assume that signals possess any semantic or 'language-like' properties.

Individuals from a wide variety of species are able to produce complex signals based on the affordances and constraints of their social and physical world, and their developmental and evolutionary histories (Tinbergen, 1963; Barrett, 2011). By considering the various modalities through which an organism can signal, the ways in which the environment constrains the signals, and the various ways in which individual signals may amplify and enhance each other, it is clear that one should perhaps expect a continuum of signals that reflect these kinds of influences, rather than a static array of stereotypical signals. This is not to say that stereotypical or ritualized signals do not exist, only that they form one end of a continuum and we should be open to the possibility of a flexible array of signals designed to manage and influence the behaviour of others, rather than a fixed 'vocabulary' of signals that have a precise "meaning" or goal.

Conceptualizing signals in this manner gets us away from more anthropocentric ways of thinking, and from seeing other organisms only in human terms.

1.3. Threat Displays and Honesty

The spontaneous agonistic interactions engaged in by male vervet monkeys, ranging from actual physical aggression to the exchange of threats, form the focus of my thesis. In the context of the above discussion of signaling, the functional significance of threat displays is obviously of interest. Threat displays are generally conceived as a form of communicative device designed to allow individuals avoid the costs of aggression; individuals can mutually assess their resource holding potential (RHP) via such displays without having to pay the costs of combat. If threat displays always prevent fighting from taking place, however, this means that weaker males may win encounters, or at least avoid physical aggression, that they would otherwise lose if an actual fight were to take place. In other words, threat displays can be dishonest, and no longer convey reliable information about RHP. Zahavi (1975, 1977) suggested that displays of any sort would need to be costly to be reliable (i.e., they would function as handicaps), such that the costs of producing them would be disproportionately high for weak individuals, so that only high-quality individuals would be able to produce them, and this would ensure that signals remained reliable indicators of RHP.

Enquist (1985), however, produced a theoretical model that demonstrated how cost-free signalling could evolve if certain key conditions were met. Most notably, he argued that it was the *potential* costs of having to fight against a stronger individual that kept displays honest. More recently, Számadó (2008) argued that there is component missing from this model, in that Enquist (1985) did not fully specify the nature of the mechanism by which such potential costs could be realized. Számadó (2008) remedied this by suggesting that proximity risk was the means by which displays could remain honest and cost-free in an evolutionary sense. Proximity works to keep displays honest because threats are only credible if they are made from a distance at which a male could actually employ his weaponry. This is because the function of a threat display is to convey information about the risk of an impending attack, i.e., the displaying individual's willingness to fight. We can think of this in human terms: if an individual threatens to hit someone from less than a foot away it is obviously a more credible threat than if they yell their intention from 12 feet away. This is because, should their opponent choose to accept the challenge, the option to surrender or run away will no longer be available. Any individual who threatens an opponent must, therefore, be prepared to follow up a threat with an actual attack, and so risk retaliation. In this way, proximity risk maintains honesty and hence evolutionary stability, as only those males of sufficient quality to actively take on opponents will be willing to engage in threat displays. Számadó (2008) further demonstrates that honest signalling is only an EES within 'the honest striking distance' of the opponent (Számadó, 2008). Outside this zone, signals may be a mixture of honest and dishonest signalling – the "dishonest striking distance"—and beyond the dishonest striking distance; signals become completely unreliable and should not be used or, if they are, ignored. Proximity between opponents therefore becomes the crucial measure when analysing the frequency, effectiveness and reliability of threat displays (Számadó, 2008).

The honest striking distance is species-specific because it depends on an animals' weaponry, which can vary in size and morphology. For example, some species use antlers as weapons, and hence antler length will determine the honest striking distance. The use of canines versus claws, or whether attacks are launched from a standing position or made on the run, similarly influence the extent of the honest striking zone. Számadó's (2008) point here is that Enquist's model (1985) would be ineffective without taking into consideration the species-specific nature of weaponry and its influence on striking distance, as without proximity risk animals would have no means of assessing the credibility of a threat.

According to Számadó (2008), threat displays were originally cues presented for fighting that have now been 'frozen into signals', which function to transfer information about RHP and aggressive intention. In contrast to this is the suggestion that "threat displays" may not be ritualized and communicative in this way, but instead represent actual attempts by individuals to exert influence over each other by aggressive means (i.e., individuals are engaged in actual combat), with the result that they become locked in an effective 'stalemate'. That is, male are, in fact, attempting to strike and block blows, using various combat tactics and counter-tactics (Pellis, 1997; Geist, 1974), and this jockeying for advantage gives rise to a situation in which males appear to be engaged in ritualized displays, because they do not actually make physical contact. As with Számadó's idea of proximity risk, this hypothesis also predicts that threats should occur at close proximity, because they represent actual attempts to wound opponents. Here, however, the threat does not operate as a "conventional" communicative signal, and displays are, by necessity, "honest" because they represent physical acts of combat.

1.4. Targets and Tactics

To expand on this idea, drawing mainly on Pellis' work (e.g., Pellis, 1997), we can see that, historically, views of combat incorrectly concluded that a lack of escalation during physical aggression reflected evolutionary pressures acting on behalf of the species, as combatants would each hold back from striking any blow that might prove fatal to their opponent (that is, animals did not attempt to strike a fatal blow because this would be detrimental to the survival of the species as a whole if individuals killed each other over resources). Once properly evaluated, however, it becomes clear that there are many examples of combat fatalities in animals (Geist, 1967; cervids, caprinids), which occur at rates much higher than expected if animals were restraining themselves, and it is also clear that, when given the opportunity to do so, an animal will strike a mortal blow to its opponent (Geist, 1974). Combat is, therefore, a synergistic interaction of animals actively 'doing their best to inflict harm... countered by the other's defense' (Pellis, 1997, pp.108). Combat is therefore "selfish" and egocentric: neither individual is acting, or withholding acts, in order to ensure the other's survival. Although the interaction often appears to be a stalemate, this is simply due to the nature of combat, and the interplay of offensive and defensive tactics to inflict and avoid blows on a particular bodily target. Thus, as noted above, many animals appear to be behaving as if they are engaging in a 'ritualised' interaction, such as a threat or dominance interaction, rather than in combat itself (Pellis, 1997). It is important to note here that a position on the adaptive significance of the behaviour itself is not needed to investigate the 'combat' versus 'communicative' elements of such displays (Lauder, 1986).

By observing combat in muriod rodents, Pellis (1997) showed that postures traditionally assumed to be signalling a fully offensive or defensive state were actually postures used to gain tactical advantage. Pellis (1997) illustrates this using the "supine" posture, which is typically assumed to signal submission. As behaviour during an aggressive interaction is unavoidably contingent on what the other animal is doing, as well as what both of the individuals have just done, it requires that each individual adjust its tactics throughout the interaction in order to not be attacked, even if they are themselves attacker. In line with this, supine postures do not merely signal submission (though it does provide optimal protection by blocking access to vital organs) because, in some cases, a supine position may actually better prepare an individual for attack. In this sense, then, the goal of adopting a supine posture can only be understood fully if it is situated in the context of the interaction. Likewise, we can consider the movements in vervet male-male interactions, such as threats, dominance and submission displays, to reflect goals that are situated in the context of the interaction, rather than reflecting a 'pre-formed' intentional goal in each individual's head.

In similar vein, Moran, Fentress & Golani, (1981) investigated ritualized behaviour in wolves, and came to the conclusion that "communication is evidenced in this study (not by the assumptions) but by the set of spatiotemporal constraints on the behaviour of the individual ..." (Moran et al., 1981, pp.1162). They also pointed out that, "unintelligible gestures can now be understood in terms of straightforward regularities along several dimensions of movement in real and interaction space". In other words, behaviours that were originally described to be heavily specialized for communication could instead be shown to reflect the manner in which one animal adjusted its postural and locomotor behaviour to reflect the movements of its partner in similar fashion to Pellis' (1997) analysis.

Foundational to this approach, then, is the idea that animals are constrained by the ways in which their bodies move, as well as the weaponry available to them. Following from this, individuals will also be constrained by the environment (social and physical) in which the interaction occurs. This affects both their chosen target of attack, and the tactics that are available and favoured during combat. Combatants may therefore rely on a simple rule of 'given the context, use the quickest or most effective manoeuvre to gain access or evade contact' (Pellis, 1997) when engaged in aggressive encounters, rather than having a fully specified set of tactics that are stored and employed in intentional fashion.

1.5 A Situated Perspective

Similar ideas regarding the 'situatedness' of behaviour had also been developed earlier by Hinde (1985) and have been expanded on more recently by Griffiths and Scarantino (2005). Hinde (1985) argued that emotions are a means by which individuals can negotiate their interactions; a point he illustrated using threat displays. His suggestion was that emotions need not always be 'expressive' of some inner (motivational) state, but may also be 'strategic', in the sense that an animal has no specific motivation, or goal-state it wishes to achieve, but instead directs a behaviour toward another animal as a means to determine what it should do next. In the context of threat displays, Hinde (1985) noted that, immediately after issuing a "threat", the displaying animal itself may often flee (and do so quite frequently). Thus, the displaying animal may not be threatening as such, but simply uncertain about what it should do next. In such cases, which of the several possible responses an animal shows next will depend crucially on the behaviour of its rival (Hinde, 1985). Thus, as Griffiths and Scarantino (2005) note, it is "undetermined whether the bird (or monkey) is angry or afraid. The identity of the emotion will be shaped through time by the responses received to the threat display." (Griffiths & Scarantino, 2005, pp. 20). In other words, as noted above with respect to postural aspects of behaviour, emotional displays are also 'situated' in the sense that each individual adjusts its behaviour according to the response of its partner and/ or other environmental factors. Another way to put it is that a threat isn't a threat until another animal responds to it as such.

In this view, behaviours that have classically been viewed as an involuntary expression of an animal's physiological state of arousal can instead (and in line with the ideas expressed above) be viewed as signals that are designed to influence the behaviour of other organisms, or as 'strategic' moves in an ongoing transaction between them. As articulated by Griffiths and Scarantino (2005), a situated perspective on cognition stresses the necessary relationship between the structure of the social world and the nature of the emotions displayed. Emotions can be produced or brought about by social and physical contexts (i.e., the standard view that emotions are 'expressive'), but they can also be used to influence the social environment itself and it is in this sense that they can be considered as 'strategic'. Moreover, 'strategic' emotions do not need to be explained by complex cognitive mechanisms that are dependent on conceptual thought. Using the example of a change in feeding behaviour by male chickens when females are present, Griffiths and Scarantino (2005) illustrate how animals need not conceptualize a goal in order to bring forth complex behavioural variation in themselves and/or others. Samango monkeys also demonstrate these kinds of effects: males engage in highly aggressive behaviour with other males, but only during the mating season when females and multiple males are forced to coexist in close proximity to each other (Henzi & Lawes, 1987). Outside the mating season, the troop returns to its one-male status, and the other males similarly co-exist peacefully in all-male groups.

Griffiths and Scarantino (2005) stress that both the expressive and strategic use of emotion can occur within a single interaction, and need not do so in unison. This perspective builds upon Rendall et al.'s (2009) argument regarding signalling, as it takes into account the fact that signalling is not a closed system that remains unaffected by the environment. If we accept that signals are "thrown out into the world" as a means to prompt a response from other individuals in an unpredictable manner (i.e., the reason for the "threat" is to reduce uncertainty about what the signaller should do next, but what the other animal does in response to the threat cannot, by definition, be predicted in advance), then we can view signalling systems as essentially open ended (Rendall et al., 2009). Vervet male interactions provide an excellent system into which to assess the value of this approach, as there seems to be no set pattern to the way in which agonistic interactions unfold. An emoter's final 'intentions' need not be known when sending signals, nor are the interactant's responses. It is an ongoing process mediated by emotions, and the signal meaning produced is therefore 'emergent' and cannot be separated from its context or the males' state of arousal.

As noted above, Griffiths and Scarantino (2005) suggest that emotions can be seen as goal-oriented without being conceptual, using von Uexküll's notion of the umwelt to do so (Uexküll, 1909). Griffiths and Scarantino (2005) give the example of how the environment of a prey animal, such as a rabbit, affords escapable opportunities as the prey's goals, and the animal perceives these as such. The prey does not have to hold these goals in its head, however; rather, they emerge and exist in real time as the prey interacts with its environment (for example, when they are being chased by a predator). A rabbit being chased by a fox sees holes as "escapes" in a way that the fox does not merely due to the nature of being a rabbit and the effect of being chased. One can make a similar argument for vervet males: a male interacting with other males need not hold their ranks in his head, but rather may only need to register his egocentric position in relation to each of them in real time, in the midst of interacting with them. That is, males may take an essentially 'second person' perspective with respect to other individuals, rather than necessarily requiring 3rd party knowledge (Reddy & Morris, 2004).

1.6. Other Views of Expressive Behaviour

Following on from the idea that there is a necessary relationship between the social world and emotional responding is Sheets-Johnstone's (1999) concept that body movements are in themselves expressive. This builds upon Darwin's (1874) work, in which he showed how involuntary, spontaneous movement (i.e. pulling your hand away from a hot stove, running when an unfamiliar sound is heard) could be viewed as adaptive, as our bodies necessarily respond (act) to our emotions.

As evidenced in the work presented by Sheets-Johnstone (Jacobson, 1967, 1970; Sperry, 1952; Bull, 1951 in Sheets- Johnstone, 1999), movement and emotion are intertwined, by which she means that they are joined, but not identical. Sheets-Johnstone (1999) further argues that movement is not only expressive, but also generative; that is, movement can *produce* emotion. For example, generative emotion is the basis of affect induction theory, in which emotion is created via synchrony in movement (e.g., Conner, Smolker, and Bejder, 2006) and facial expressions (Bouguys, Bloem &Groothuis, 1995). It is in the entanglement of emotion and movement that we can see most clearly that the brain is first and foremost an organ that moves muscles. In other words, the brain did not evolve to merely register representations about the world but, rather, it evolved for adaptive action and behaviour. Brooks (1989) illustrates this perfectly in his robotics work (also see Barrett, 2011). By exploiting the structure of the environment, and that of their own bodies, Brooks creates robots that require very little in the way of central processing, but which are nevertheless very flexible as their behaviour is "coupled" to the environment, such that the environment forms part of the cognitive system and itself helps produce adaptive functional behaviour.

Sheets-Johnstone (1999) suggests that movement and emotion are intertwined, mutually congruent, and experienced holistically. She suggests, therefore, that they are usually divisible only upon reflection. The ability to divide movement from expression is possible during real time, but most often occurs as a learned response, by means of inhibition or redirection (replacing an emotional response and/or a movement). Examples of this from vervet behaviour may be their ability to control submissive acts, such as chutters and lipsmacking, rather than simply retreating when an individual of higher rank is in proximity. In this sense, Sheets- Johnstone (1999) point is similar to both Griffith and Scarantino's (2005) position and that of Hinde (1985): emotions can be expressive but also strategic. Sheets-Johnstone (1999) is also of the view that signals did not evolve for the purpose of communication first and foremost, but are more concerned with motivating action, a perspective similar to Pellis (1997) and Pelllis & Pellis (2011). In this way, we can see how researchers from a variety of perspectives, from ethology to philosophy, have converged on similar views with respect to the situated and embedded nature of emotion and behaviour.

1.7. Aims of Thesis

The aims of this these are, first, to assess the targets of combat, and construct a qualitative description of offensive and defensive tactics used during physical aggression. Second, it aims to test whether males initiate and maintain certain orientations and postures that defend these targets against attack, and assess whether any such patterns show rank-related effects. Third, to test whether contextual factors predict the occurrence of high aggression. Fourth, to test whether proximity influences male behaviour in agonistic contexts as predicted by Számadó (2008) and whether threat display curves (i.e., the probability of threat frequency with increasing distance) reflect differential performance of different threats at different distances. Fifth, and finally, to test whether male threat displays show any evidence for ritualization or whether they are inherently unpredictable.

CHAPTER TWO:
METHODS

2.1. Vervet Monkeys: General Overview

Vervet monkeys (*Chlorocebus aethiops*) are medium-sized, semi-terrestrial monkeys belonging to the sub-family *Cercopithecenae.* They are found throughout Africa, from Senegal to Ethiopia and Sudan to the tip of South Africa (Tappen, 1960). Vervet populations are also found on the Caribbean islands of St Kitts, Nevis and Barbados as a consequence of human colonization (Fedigan & Fedigan, 1988). Across Africa, they are found in a wide variety of habitats, ranging from semi deserts, to savannah, rainforest edge, gallery forests, and even urban areas, excluding only rain-forests and desert habitats (Chapman & Fedigan, 1984). They are most common in riverine forest and woodland areas as they are thought to be heavily water-dependent, and thus require habitats that supply ready access to water (Wrangham, 1981; but see McDougall, Forshaw, Barrett & Henzi, 2010 who report that vervets can survive for at least a month in the absence of any free-standing water). Potential predators of vervets include felines such as the lion, leopard, cheetah, caracal, African wild cat, serval, as well as the hyena, black backed jackal, baboon, raptor, and humans (Enstam & Isbell, 2002).

In contrast to the closely related forest-living guenons (monkeys of the genus: *Cercopithecus*), which tend to form one-male/multi-female groups, vervets live in multi-male/multi-female groups, that range in size from 5 to 76 individuals, with a mean of roughly 25, and an adult sex ratio of 1M: 1.5F (Fedigan & Fedigan, 1988). Females remain in their natal group throughout their lives, hence groups are matrilineally structured and females tend to maintain their relative ranks throughout their lives as part of a stable, linear dominance hierarchy (Struhsaker, 1967a). Males disperse from their natal units at or around sexual maturity (average age 5) and continue to transfer between troops approximately every three years throughout adulthood (Henzi & Lucas, 1980). This movement by males introduces less stability into male relationships and dominance hierarchies. Male dominance is regularly tested and re-negotiated with individuals from non-natal groups (Henzi & Lucas, 1980). Male adult vervets direct most of their aggression towards other males (Baldellou & Henzi, 1992), and self-initiated displays of subordination by lower ranking to higher rankings males are common (Henzi, 1982). These self-initiated displays, or 'homage', are suggested to decrease potential aggression from higher ranking males. Males are generally tolerant of each other within troops, and male-male grooming, while making up a small proportion of their overall time budget, is observed (see e.g., Freeman, Sashaw, Barrett & Henzi, 2012).

Vervet monkeys are territorial, but the degree to which they defend their territory against neighbouring troops varies with seasonal fluctuations in resource availability (Chapman & Fedigan, 1984; Personal obs.). Inter-troop encounters at territory boundaries can therefore range from intensely agonistic to mildly associative. Territory sizes range from ≈ 0.32 km^2 on St. Kitts (Chapman & Fedigan, 1984), to 1.78 km^2 in Senegal (Harrison, 1983). The size of territory reflects both habitat quality and vegetation type (De Moor & Steffen, 1972; Struhsaker, 1967a). With respect to diet, vervets are opportunistic omnivores: they feed on a wide variety of plant species, insects and occasionally bird eggs and chicks (Struhsaker, 1967a). Vervets also adjust their diets often according to seasonal fluctuations in availability, although they have strong preference for plants and flowers (Fedigan & Fedigan, 1988). Various species of *Acacia* are an important component of the African monkeys' diet (eg. *Acacia xanthophloia* and *Acacia tortilla*) Struhsaker, 1967a; Whitten, 1983; Wrangham & Waterman, 1981).

2.1.1. Physical Features

Vervet monkeys are mildly sexually dimorphic in size, with females approximately two thirds the size of males. Females reach an adult mass of 2.5-3.5kg and an average body length of 37cm, while males weigh 4.1-5.8 kg, with an average body length of 41 cm (Bolter & Zihlman, 2006; Turner, Anapol & Jolly, 1994, 1997). Males can also be distinguished by a bright blue scrotum, which contrasts with a red penis and peranius and the white coat of their underside. The skin of a vervet monkey is black on its face, limbs and back, but light blue on the abdomen. They are covered with a short coat of grey fur, which has a marked 'grizzled' appearance in males. Like all Cercopithecines, vervets possess cheek pouches and their ischial callosities are small and well separated.

2.1.2 Behaviour during the Mating Season

Vervet monkeys are seasonal breeders, with a clearly defined mating and breeding season among wild populations. In Amboseli, Kenya, the May to October mating season occurs during the dry season, and the birth season is October to March, with a peak in November (Struhsaker, 1967b). The vervets in our study population are similar to the Amboseli vervets, with copulations observed between April and August, with a peak in May

(Freeman, Pasternak, Rubi, Barrett & Henzi, 2012). During this period, in addition to actual copulations and copulation attempts, males are also observed probing a female's ano-genital region, as well as following a female around for long periods throughout the day. In addition, male-male behaviour changes markedly during the mating season. Males become more aggressive and impulsive, engaging in significant numbers of dominance interactions with other males (Henzi & Lucas, 1980). This includes an increase in so-called dominance displays, threats, chases and fighting, as well as coalitions (Freeman et al., 2012). There is also an increase in affiliative behaviour between males, most notably grooming. The mating season is also a period of high male immigration and emigration. This results in a higher proportion of new, peripheral males moving into and out of troops ("influx" males) (Struhsaker, 1967b; Lawes & Henzi, 1995). Both these factors may account for the rise of dominance interactions and aggression during the mating season, as the entry of new males and the emigration of resident males has a marked effect on the stability of the male dominance hierarchy.

2.2 Study Site

I collected data as part of an ongoing study of the vervet monkey population in the Samara Private Game Reserve, Eastern Cape Province, South Africa ($32^0 22'$S, $24^0 52'$E. Figure 2.1). The reserve comprises 34,000ha of mountains and nama-karoo grassland transected by the Milk River and its tributaries. Our study site is located in the north of the reserve where the river, which flows only intermittently, has not been dammed and where the monkeys have no access to artificial water sources. Such point sources of water have been established away from the river and there are generally vervet groups associated with them. The area receives a declining average of 330mm rain per annum (Wet season: October-March; Dry season: April-September) and experiences a mean maximum temperature of 27^{0}C and a mean minimum temperature of 10^{0}C (Figure 2.2.). The coldest month is July when snow falls on the surrounding mountains (mean minimum: 4^{0}C), while December and January are the hottest (mean maximum: 34^{0}C).

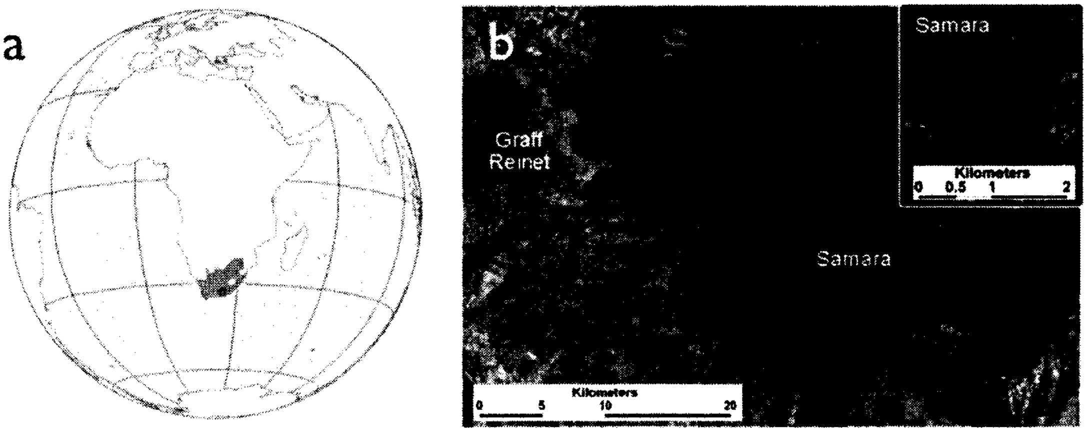

Figure 2.1. Location of the general study area (a) within South Africa and (b) in relation to the town of Graaff Reinet. The rectangle indicates the study site (enlarged in the inset). Adapted with permission from Pasternak (2011).

In addition to a variety of ungulates, the reserve has an established predator guild. Animals that prey on the study population include cheetah (*Acinonyx jubatus* Brookes), caracal (*Caracal caracal* Schreber), black-backed jackal (*Canis mesomelas* Schreber), martial eagle (*Polemaetus bellicosus* Daudin), Verreaux's eagle (*Aquila verreauxii* Less.) and both the giant (*Bubo lacteus* Temminck) and Cape eagle owl (*Bubo capensis* Smith). While there are no large constrictors in the region, venomous snakes were also a significant source of mortality.

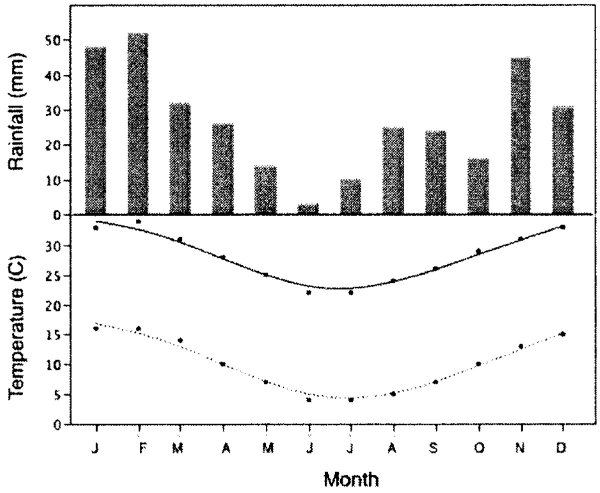

Figure 2.2. Long-term mean monthly rainfall and temperature (mean minimum T°C: dotted line; mean maximum T°C: solid line) data for the study site. Adapted with permission from Pasternak (2011).

The mean size of vervet troops at Samara (based on counts of 29 troops) is 26.62 individuals, which is comparable to other populations. Troops can, however, be distinguished by whether their ranges are centred on the river or whether their source of water is artificial and maintained by humans. River troops (N=15) are significantly larger mean size (40.13+/-15.53 S.D.) than troops relying on human-provided water (N=14. Mean=12.14 +/-3.23 S.D.) (Pasternak, 2011).

2.3. Study Animals

I collected data on males from two large, river-based troops (RST: N = ~ 72 animals and RBM: N = ~ 48 animals) across the peak of 2009 and 2010 mating seasons (10 consecutive weeks from mid- April to Mid-June in each year). The modal adult sex ratio (M/F) during 2009-2010 was 0.67 for RBM (N_{MALES}=10, $N_{FEMALES}$=15) and 0.43 for RST (N_{MALES}=10, $N_{FEMALES}$=23) (Pasternak, 2011). Both troops were fully habituated to human presence, and have been so since 2008.

2.3.1 RST

RST followed a generally predictable daily route, sleeping in the same sleep-site each night. During the day, they remained close to the riverbed, feeding mainly on *Acacia karoo*. The troop interacted frequently with RBM, as well as two other neighbouring troops (SWT and PCNC) and occasionally encountered a third troop (HCT). During 2009, all standing water in RST's territory dried up, and the troop moved beyond their normal range to an alternative water source (McDougall et al., 2010). This travel entailed crossing an open plain which left them more exposed to potential predator attacks. The troop continued to frequent this alternative water site throughout the 2010 mating season. The home range of RST therefore expanded from 25 ha at the beginning of 2009 to 63.7 ha in 2010 (McDougall et al., 2010; Pasternak, 2011).

At the beginning of the 2009 mating season, RST was composed of 10 males and two sub-adult males. As the season progressed, the troop gained eight extra troop males, while two resident males emigrated, although one of these returned to RST at the end of the mating season. Four extra troop males remained in the troop for a significant period, but left within the bounds of the mating season. Between the mating season of 2009 and that of 2010, another four males emigrated from RST, and two males immigrated into it. Thus, in 2010, 11 of the males from the previous year remained. As the season progressed, one resident male emigrated and the troop gained four extra troop males, two of which left again during the mating season. At the end of the 2010 mating season, RST contained 12 males.

2.3.2. RBM

RBM varied its daily schedule throughout the mating season, using four different sleep sites. This troop spent more time in open habitat and, like RST, they travelled to a new water site when other water sources in their range dried up during 2009. RBM regularly encountered five other vervet troops (PCNC, LDT, RST, SWT and HCT) with the latter two troops often being present at the water site. As with RST, RBM home range was approximately 25 ha in 2009, but had increased to 167.1 ha in 2010 (McDougall et al., 2010; Pasternak, 2011).

Ten males were present in RBM at the beginning of the 2009 mating season. Four males then emigrated, with three returning by the end of the mating season. RBM gained one influx male during the mating season; a male that transferred from RST. Between the 2009 and 2010 mating seasons, five males emigrated from RBM. At the beginning of the 2010 mating season, then, RBM contained four males from the previous season, and had gained one extra troop male. Two natal males also reached sub-adulthood, and were therefore included as part of the male hierarchy. During the mating season, RBM experienced an influx of five extra troop males that joined for an extended period, four of which were still present at the end of the mating season. The two natal males transferred together to RST. By the end of the 2010 season, eight males remained in RBM.

2.4. Data collection

2.4.1. Video-recordings

During both the 2009 and 2010 mating seasons, I collected video-recordings of male-male social interactions from both troops during dawn to dusk follows (approximately 6.30 to 17.30) on each day of data collection. During the 2010 season, I also collected data on male spatial position using GPS (not presented as part of this thesis), which necessarily reduced the number of video-recordings collected relative to 2009. Troop follows alternated every two consecutive days, averaging 10 days of data collection on each troop per month. On each day of data collection, individual males were followed and filmed at a distance of approximately five metres by myself and, during the 2009 season, a field assistant (David McCaffrey), who followed an identical protocol. Filming began whenever another male was present in the vicinity and potentially able to interact. Video-recordings were made using a Canon digital video camcorder (Model ZR950), and stored on tape during the 2009 season and on SD card during 2010. Males were selected according to a predetermined schedule generated prior to the beginning of data collection (usually the evening before). A random number generator was used to produce the order in which males were to be followed on any given day. If a focal male had not interacted with any other male after 10 minutes of continuous following, we moved onto the next male on the list. Males could be identified via distinguishing features, such as scars, unique facial and body markings, tail morphology and gait patterns. Additional information about an interaction, such as identification of individuals involved, location, time and date, were noted verbally on the video recording.

Table 2.1. Summary of males present in the two study troops (RST and RBM) during the 2009 and 2010 mating seasons.

SAMARA MALES 2009-2010

Troop	Male ID	2009 Rank	2009 David's Score	2009 Mating season movement	Non-mating season movement	2010 Mating season movement	2010 Rank	2010 David's Score
RST	OR	1	14.03				2	14.19
	AJ	2	11.97				1	19.46
	SP	3	11.87				6	12.02
	JU	4	10.93			Transfer out	3	13.02
	BU	5	10.88				5	12.51
	LA	6	10.31	Transfer/Return	Transfer out		X	X
	CH	7	9.47	Transfer out			X	X
	FO	8	9.47	Extra			X	X
	QU	9	9.43		Transfer out		X	X
	JA	10	8.9	Transfer in	Transfer out		X	X
	HX	11	8.9	Extra			X	X
	RI	12	8.72	Transfer out			X	X
	GO	13	8.72	Transfer in			4	12.96
	JI	14	8.64	Extra			X	X
	KO	15	8.31				8	10.1
	WA	16	8.12	Transfer in			X	X
	BO	17	8.1	Transfer in			7	10.48
	DO	18	8.06				10	8.9
	DY	19	7.31			Transfer out	X	X
	OZ	20	6.85	Transfer in			9	9.94
	PA	X	X			Transfer in	13	8.15
	MU	X	X			Transfer in	12	8.56
	TO	X	X		Transfer in		11	8.95
	GR	X	X			Extra	X	
RBM	CA	1	7.77				2	7.65
	AL	2	6.92		Transfer out		X	X
	VI	3	6.32				1	7.97
	IG	4	5.13	Transfer/Return	Transfer out		X	X
	FR	5	4.71		Transfer out		X	X
	DA	6	4.71	Transfer out	Return		3	6.94
	LC	7	4.5	Transfer out			X	X
	ED	8	4.5		Transfer out		X	X
	JI	9	4	Transfer out	Return/Transfer out		X	X
	HA	10	3.43				7	4.24
	CH	11	3.09	Transfer in			X	X
	TA	X	X			Transfer in	10	2.47
	WY	X	X			Transfer in	6	4.76
	BL	X	X			Extra	9	3.55
	ST	X	X			Transfer in	4	5.36
	KP	X	X			Transfer in	5	5.05
	EG	X	X			Transfer in	8	4.07

2.4.2. Ad libitum records

A daily record was kept of general troop activity, general path travelled, extra troop interactions, as well as any behaviours of interest within the troop. The latter included mating behaviour, as well as any displacements and supplants by the males. Wounds were recorded for all males. *Ad libitum* samples do not yield random samples of behaviour of all troop individuals, but it was assumed that the random sampling of dyadic agonistic interactions was comparable to all samples of the dyad.

2.5. Data Analysis

In what follows, I provide details of the general analytical procedures followed. More specific methodological details are provided in the specific chapters in which a particular analysis appears.

2.5.1. Assessment of Male Dominance Rank

Dominance was calculated on the basis of summed interactions and supplants/displacements of one individual by another. Observed agonistic behaviour between males came from both 10 minute focal follows and ad libitum samples. These data were combined data collected by other researchers at the site. For 2009, data were also collected by Nicola Forshaw, Petra McDougall, Dave McCaffrey. Ranks were calculated using Normalized David Scores (De Vries & Stevens, 2006). A total of 979 male-male interactions were recorded across both troops for 2009-2010. David scores of males during the 2009 and 2010 mating seasons are given in Table 1.

2.5.2. Video Database Construction

Forty-six hours of video were collected in the field (2009), followed by an additional 6 hours in 2010. I uploaded video recordings to computer using Apple iMovie'09 (Version 8.0) software. I then edited each video, removing footage that did not contain any male-male interactions and then converted recordings to mpeg files. I then labelled each video file with a unique identifying code, which I also entered into an Excel spreadsheet, along with information on the date and time of the recording, season (2009 or 2010), troop identity and identity of the data collector (AT or DM). I then reviewed each video file and added further information on each behavioural interaction sequence to the spreadsheet. Specifically, I added a brief description of the interaction from start to finish, including details of dyadic displacements, male postures, displays, threats, fights affiliative behaviour and copulations, the distance between the males at each point in the sequence, and the identity and number of other monkeys present in the vicinity. In this way, I created a searchable inventory/database of all behavioural interaction sequences in my video library. I used the ethograms developed by Struhsaker (1967b) and Henzi (1982) to describe and classify behaviours and interaction sequences (Table 2.2.). Both) Struhsaker (1967b) and Henzi (1982) placed behaviours in categories of 'threats', 'dominance' and 'submissive' behaviours, and I followed this convention in my descriptions, and present them as such in Table 2.2. It is important to note, however, that as one of my aims in this thesis was to test whether particular behaviours really do constitute 'threats', for the purposes of analysis, I used more neutral behavioural descriptions to classify the behaviours when subjecting to detailed frame-by-frame analysis (see below).

2.5.3 Video Analysis

The video database contained a total of 291 dyadic interactions, 109 of which contained threat displays of some description. From these, I selected interactions that had been recorded in their entirety (i.e., from one male's initial approach until the end of the interaction, when the males had moved apart by more than 10m), and which contained fights (i.e., one or both males struck a physical blow at the opponent), high aggression (i.e., males engaged in chasing and lunging behaviour, but failed to strike a blow) and/or threats (i.e., males engaged in behaviours defined as threats by Struhsaker, 1967b and Henzi,1982). This produced a sample of 90 interactions suitable for analysis, details which of which are given in Table 2.3.

Table 2.2. Ethogram for vervet monkeys used in this study. Comparison was made between three field studies: Amboseli, Kenya (Struhsaker (1967b); Durban, South Africa (Henzi, 1982) and Samara, South Africa (this study).

Category	Behaviour	Description	Amboseli	Durban	Samara
Threat					
	Ground (eyelid flash, stare)	Exposure of lighter coloured eyelids; maintenance eye contact.	X	X	X
	Ground (crouch)	Forequarters bent, usually while delivering an eyelid flash.	X	X	X
	Headbob	Jerking, or bobbing head on a saggital plane, usually while delivering an eyelid flash.	X	X	X
	Bipedal	Jerking, or bobbing, the body from a quadrapedal to a bipedal position. Can include delivering an eyelid flash.	X	X	X
Submissive					
	Vocalizations	Lipsmacking; chuttering	X	X	X
	Cowering	Subordinate individual lowers head/ body and avoids eye contact. Usually includes submissive vocalizations	X		X
Dominance					
	"Red, White, & Blue" Display	Dominant individual circles (or paces back and forth beside) subordinate individual with tail lifted, exposing genitalia. Subordinate individual is usually sitting and vocalizing.		X	X
	Broadside	Dominant individual stands perpendicular to subordinate, pauses, then moves on. Tail may be raised. Subordinate is usually sitting.		X	X
	Hand-on-Head	Dominant individual places hand on subordinate individuals head. These often occur in conjunction with RWB displays.			X
	Tree Display	Dominant male races through trees creating noticeable noise during inter-troop encounters.	X	X	X
Affiliative					
	Grooming	One individual combs through the fur of another individual, using its fingers. Removes parasites and debris from fur.			X

Table 2.3. Sample size for behavioural interaction sequences analysed for this thesis.

Category	# of inter-actions	# males	mean inter-actions per male	min # of inter-actions per male	max # of inter-actions per male	# dyads	average # of inter-actions per dyad	min # of inter-actions per dyad	max # of inter-actions per dyad
Low intensity aggression (threats only)	56	30	3.7	1	12	47	1.2	1	3
High intensity aggression	24	21	2.3	1	7	21	1.1	1	2
Fights	10	13	1.5	1	3	10	1.0	1	1

I subjected these video data to detailed frame-by-frame analysis, which included the use Eshkol-Wachmann movement notation (EWMN) (Eshkol & Wachmann, 1958; Moran et al., 1981; Pellis, 1997, 2011). In this system, individual movements are recorded as descriptive coordinates on an abstract sphere that represent the amount of movement made by individual limb segments. Scoring was validated by Sergio Pellis recreating the movements from the notation alone, without any knowledge of the original behaviour. Importantly, EWMN permits the description of behavioural patterns to be described via different frames of reference: one can analyse the same movement "partner-wise" (the descriptive coordinates are defined by the momentary position of the social partner), "environment-wise" (the descriptive coordinates are defined relative to the external environment), and "body-wise" (the descriptive coordinates are defined relative to the body of the individual being scored). This enables the temporal and spatial structure of behaviour to be captured in an objective and systematic fashion. Judgements or predictions about the goal of the behaviour can therefore be suspended until after the interaction is scored (Moran et al., 1981; Pellis, 2011).

Partner-wise notation means that movements made and positions held are not just descriptive of one animal, but provide a measure of the movement of both individual, and I considered this to be particularly appropriate given my project aims. I therefore used a modified (i.e., simplified) EWMN taking a partner-wise frame of reference to identify patterns of relational movement in male-male behavioural sequences. These were then used to formulate the specific hypotheses and predictions tested.

I used the software program ELAN (EUDICO Linguistic Annotator, Version 4.1.0, Lausberg & Sloeties, 2009) to score the frequency and duration of a variety of absolute and relative measures of male-male engagement (not all of which were used in this thesis). Specifically, I recorded the following absolute measures:

(i) **Velocity:** each male's speed of movement, measured in body lengths travelled per second.

(ii) **Body posture**: eight postures were scored and defined as follows:

a. *Sit-Hind*: sitting with forearms off the ground, hind legs bent, with ischial callosities contacting the substrate.

b. *Sit-Haunch*: sitting with forearms touching ground, hind legs bent, with ischial callosities contacting the substrate.

c. *Legs-Up*: sitting with callosities contacting the substrate, with arms and hind legs extended out in front. Legs often extended above chest height.

d. *Sit-Splay*: Sitting with forearms off the ground, callosities contacting the substrate, and hind legs extended/ semi-extended exposing scrotal area.

e. *Stand*: adopts a quadrupedal posture, with arms and legs straight and contacting the substrate.

f. *Crouch*: adopts a quadrupedal posture, with either/both arms and legs bent and contacting the substrate.

g. *Lying down*: either prone, supine or on their side.

h. *Bipedal*: standing vertically, with arms off the ground, and feet contacting substrate.

(iii) **Habitat location**. This was categorized as follows: (a) Ground-Bush (animal was on the ground in area dominated by bush species) (b) Bush-1 (animal was in a bush 1-3 metres in height (c) Bush-3 (animal was in a bush above 3m in height) (d) Ground-Tree (animal was on the ground in area dominated by tree species) (e) Tree-1 (animal was in a tree 1-3m in height) (f) Tree-3 (animal was in a tree above 3m in height) (g) Tree-5 (animal was in a tree above 5m in height).

(iv) **Number of other individuals present**: the number of other male, female and juvenile monkeys present in the video.

I also took three relative measures based on my modified EWMN, following Moran et al. (1981):

(i) **Relative distance**: the distance between individuals measured in monkey body lengths, ranging from 0-8. See Figure 2.3.

(ii) **Point of opposition**: the point on each animal's body to which the social partner was nearest. This does not necessarily imply any physical contact between the interactants. Changes in point of opposition can be produced by movements of either or both animals, and a single change in opposition could result from a number of distinct combinations of movements by each interactant. Point of opposition was scored as follows: 0 = head, 1 = shoulder, 2 = torso, 3 = haunch, 4 = rear. See Figure 2.3.

(iii) **Relative direction**: the orientation of each animal described relative to the simultaneous orientation or angle of the social partner. This was scored by, figuratively speaking, superimposing the body position of Male 1 directly on top of Male 2 and then scoring the relative orientation as follows: 180^0 = the first male is oriented 180^0 degrees relative to the second male in schematic space, in an anti-parallel position. In reality, the males would be facing each other; 135^0 = the first male is oriented at 45^0 toward the head of the second male, in reality, the first male would be oriented away from the second male; 90^0 = the first male's is oriented in schematic space perpendicular to the second male's body. In reality, the first male would be perpendicular to the second male; 45^0 = the first male is oriented at 45^0 in schematic space toward the second male's haunch. In reality, the first male would be facing toward the second male's head; and 0^0 = the first male is oriented at 0^0 relative to the second male in schematic space in a parallel position. In reality, the males would be facing away from each other. Changes in this variable could be the result of movements by either animal or both animals simultaneously. See Figure 2.3. As noted above, details of the specific analyses used to test hypotheses and predictions are presented in the relevant data chapter.

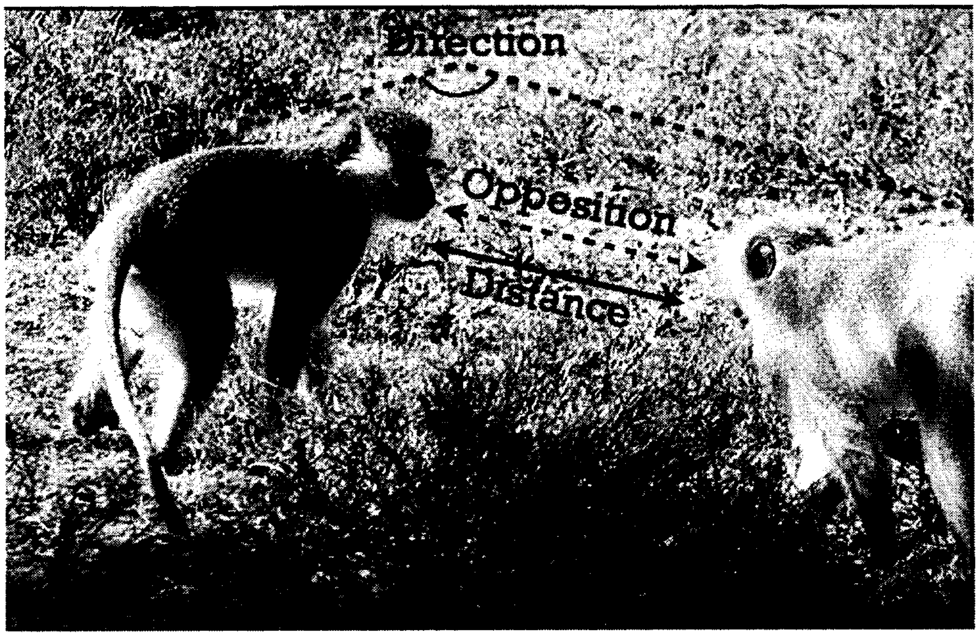

Figure 2.3. Illustration of measures used in the Modified EW annotations. Direction captures the relative angle between the opponents, opposition captures the closest relative body part, and relative distance between individuals.

CHAPTER THREE:
WOUNDS AND WEAPONRY

3.1 Introduction

As explained in Chapter One, understanding the extent to which threat displays in male vervets reflect a "strategic" versus "expressive" use of emotion (or both) requires some consideration of whether threats are conventional signals, indicating the potential for aggression (communication hypothesis), or whether they are aggressive acts in and of themselves (combat hypothesis). A combat hypothesis predicts that the function of the manoeuvres used during a threat display should directly benefit the threatening individual in offensive terms (increasing their ability to injure their opponent) or defensive terms (protecting themselves from attack) (Pellis, 1997). In contrast, a communication hypothesis holds that the function of manoeuvres used during a threat display are designed to inform the opponent of the threatening individual's resource holding potential (RHP). As such, the signals used need not necessarily include any elements drawn from actual fighting tactics: any display that indicates male strength or endurance could function effectively under such circumstances.

As put forward by Számadó (2008), however, the key element that keeps threat displays honest is inter-individual proximity. Males should therefore display at a distance that represents a credible threat: that is, displays should occur within a radius dictated by the nature of male weaponry. Furthermore, Szamado (2008) argues that an individual should indicate both its readiness and willingness to attack, such that threatening individuals should deploy their weaponry in much the same way that they would during an actual fight. Both hypotheses, therefore, predict that the relative distance between opponents is key to determining whether 'threat displays' occur, and that such displays should reflect actual fighting tactics. If males display at distances beyond the range at which they can present a credible threat, their displays can be considered as 'dishonest' and opponents should disregard them.

One important point to make, then, given this assessment, is that the combat and communication hypotheses are not necessarily mutually exclusive; that is, a display of weaponry at the appropriate proximity may well function, in an evolutionarily sense, to keep displays honest by indicating readiness to fight, but, of course, males that are displaying their weaponry in such a fashion may not be simply displaying their *future* willingness to fight, but may be engaged in actual aggressive combat behaviour. That is, the *immediate* function of the behaviour may also be to attack and cause injury to the opponent. Given that the opponent is attempting to achieve something similar, then, as males simultaneously attempt to block their opponents while attempting to deliver a strike themselves, this give rise to what appears to be well-balanced, 'ritualized' threat behaviour (Pellis, 1997). In this way, the evolutionarily functional analysis maps onto the "immediate" functional analysis of Pellis, with proximity as the link.

In addition, if we take on board Griffiths and Scarantino's (2005) 'situated cognition' approach, we need to consider the possibility that the occurrence and outcome of particular types of male-male interactions may be influenced, or even determined, by contextual factors. Along these lines, Reinhart, Pellis, Theirry, Gauthier, VanderLaan & Vasey (2010) showed how the differences in the target and tactics used during play fighting by Japanese versus Tonkean macaques could be traced to differences in social structure, with the more 'despotic' Japanese macaques displaying a more competitive play fighting style compared to the more 'egalitarian' Tonkean macaques, which show a more cooperative play-fighting style (see also Pellis, OBrien, Pellis, Teitelbaum, Wolgin & Kennedy (1988) for an example of house cats in changing targets and tactics in different predatory settings). In the case of male vervets, it seems reasonable to hypothesize that elements of the social situation relating to mating effort could affect the nature of male interactions; these would include factors such as the number of females present (which may increase male willingness to escalate aggressively and drive their opponent off, if this increases the chances of mating access); the number of other adult males present (which may decrease male willingness to escalate by increasing the risk of coalition formation by their opponent); and habitat type (which could, for example, impede males' ability to escape their opponent or increase the likelihood that other animals can see the interaction, leading to 'audience effects'). The relative rank of males can also be considered as a factor as, although not contextual in a standard sense, it reflects the relation between two males, rather than some absolute quality of the males themselves (although, of course, their position in the hierarchy may depend on such qualities). For example, low ranking males may initiate interactions with higher ranking males as dominance challenges (which would then lead to such males securing a higher probability of mating), and so these kinds of interactions may be more likely to escalate into actual aggression as there is more at stake. Rank distance between males may be key in this respect: more closely ranked males may also be better matched physically, and so more likely to engage in physical tests of the relationship, compared to more distantly ranked animals, where the bounds of the relationship are more clearly marked and/or low ranking males are more likely to de-escalate aggression because of the risk of other males supporting the dominant in a coalition (which is the most common pattern seen in male-male coalition formation: Bissonette et al., unpublished).

3.2. Wounds as Predictors of Targets during Combat

Identifying those area(s) of the body that form the target(s) during combat is a natural first step in any analysis of this kind, as a proper understanding of the nature of the target area allows one to predict the range of bodily actions and responses that males are likely to produce as they attempt to reach the target and protect their own target areas. Identifying the target area also allows for an assessment of whether, when in proximity, individual males are always attempting to inflict injury, or whether they are producing some form of ritualized display designed to signal submission, or otherwise allow males to assess their relative RHP.

Previous studies have used wound counts as a means of identifying the possible target areas on the assumption that wounding will occur more frequently in those regions that are actively attacked by opponents during actual fighting and during play fighting (e.g., Geist, 1967, 1986; Foreman & Brain, 2006; Pellis, 1997 [combat]; Pellis & Pellis, 1997; Reinhart et al., 2010 [play fighting]). I follow a similar procedure here, with the assumption being that the primary target should receive the most hits. It is important to remember, however, that as an agonistic encounter involves the inter-play between two partners with the intention to inflict harm (unlike play fighting), individuals will not always reach their preferred target because of the defensive manoeuvres of the social partner which may influence the number of hits that meet the preferred target area.

Targets are generally species-typical because differences in morphology and weaponry both enable and constrain the possibilities for particular kinds of movement or forms of attack, thereby making certain areas of the body more vulnerable to injury and easier to target. Cervids, for example, possess antlers and are thus able to deliver an effective blow to their opponents body, but their ability to both restrain an opponent and deliver a blow is greatly constrained compared to, say, rodents and primates, whose paws and hands give them greater freedom to hold, pin and push a partner (Geist 1974,1986). Another example is the lack of upright defensive postures in guinea pigs, which is suggested to reflect the relative weakness of this species' hindimbs and their large body mass (Grant and Mackintosh, 1963). Even within specific taxa, where morphology is often similar, there can be variation in target location. Pellis & Pellis (1997) demonstrate that, during play-fighting, ring-tail lemurs target the torso, specifically the back, while Patas monkeys target the head and neck in addition to the forelimbs, and spider monkeys bite any exposed body area within reach. Spider monkeys grapple with their partners using all four limbs plus the tail (which, being prehensile, can be used as an extra-limb), which may reflect the greater arboreality of spider monkeys compared to Patas and ring-tails, both of which are highly terrestrial, and can more effectively target specific areas using a standing or bipedal posture more effectively. Given the terrestrial habits of vervet monkeys, and the nature of their weaponry, which consists of their teeth and hands, I predict that, like Patas monkeys, vervets will target the head and neck area, and the forelimbs, and that wound distribution will reflect this choice of target.

3.3. Targets and Tactics used during Combat

As the above example illustrates, an understanding of a species' morphology and habits not only informs us of their preferred targets, but also of the various tactics they will favour during physical interactions. Pellis (1997), in a study of muroid rodents, showed how variations in the biomechanics of an animal's body can affect the tactics used to ward off an opponent, specifically, the tendency to rotate to a supine position (i.e., for the animal to lie on its back), and so remove the target area (the rump) from attack. Whereas hamsters make frequent use of this tactic during aggressive encounters, voles do so only rarely. Pellis (1997) compared six rodent species (montane voles, prairie voles, house mice, grasshopper mice, golden hamsters and Djungarian hamsters) on their tendency to rotate to a supine position and an index of their body proportions (head and body length divided by body weight). Low ratios are indicative of a squat body shape, whereas high ratios indicate an elongated body. Hamsters were found to have the smallest body ratios and the highest tendency to rotate to supine, whereas the reverse pattern was true for voles. Pellis (1997) explained this pattern by suggesting that, as rotations begin at the head and move down the body, longer-bodied animals would take longer to recruit the pelvis and so complete the rotation. Frame-by-frame analysis of rotations in prairie voles and golden hamsters showed that this was the case: the shorter bodied hamsters recruited the pelvis an average of 20s faster than the voles, and were able to withdraw their rump faster when using a supine defense. For the longer bodied voles, rotating laterally, rather than rolling over, allowed them to administer a retaliatory bite more quickly, in one fluid movement, whereas for the hamsters, a similar move requires a sequence of body movements to precede the bite. The use of a supine defense tactic is clearly related to body morphology, regardless of whether it occurs due to inherent advantages, or because the alternatives are less viable.

In the vervet case, the ability to strike a blow with the forearms is enhanced when animals are standing bipedally, even though this exposes the more vulnerable torso. I therefore predict that blows will be struck from a bipedal position, and that opponents will use tactics designed to protect their head and neck. As described in chapter 1, the brightly coloured genitalia of male vervets have been shown to play a role in signalling, and higher-ranking males more frequently display to lower-ranking males (Henzi, 1982). The genital region is also highly vulnerable to damage, however, and one would predict that males would attempt to prevent other males from attacking this area. Accordingly, we can predict that males will use tactics designed to protect their genitalia, namely, maintaining a face to face orientation, and that males that are being attacked will be more likely to adopt postures (e.g., sitting down or resting on their haunches) that obscure their genitals from their opponent and/or to hold such postures for longer durations. This, in turn, suggests that although target location can be predicted to be the head, neck and shoulders, as seen in the similarly terrestrial and closely related Patas monkey, it is possible that this target arises because males are attempting to protect more vulnerable areas of the body, i.e., that, in a sense, the head, neck and shoulders form a secondary target as males orient themselves in ways that preclude attacks to the vulnerable genital regions. Given Henzi's (1982) findings, it also seems reasonable to predict that relatively lower ranking males will be more likely to adopt and hold such postures, relative to their higher ranking opponents.

3.3. Overview of chapter

The goals of this chapter are to: (i) assess the targets of combat during fights, (ii) provide a qualitative description of offensive and defensive tactics used by males during highly aggressive interactions (i.e., those involving physical contact and/or chases), (iii) test whether males initiate and maintain a particular orientation and/or adopt certain postures during such encounters (iv) determine whether there are any contextual factors that predict the occurrence of high physical aggression (chases and fights) compared to encounters that involve threat displays alone and, finally, (iv) conduct an initial test to determine whether proximity is a factor influencing male behaviour in an agonistic context, as predicted by Szamado (2008).

3.4. Methods:

Two habituated troops of vervet monkeys (RST and RBM) were followed during two mating seasons (April through July 2009/ 2010) and interactions between males were video taped using a semi-systematic focal sampling procedure (see Chapter 2 for details). All videos were compiled into a database and general information about the interaction was recorded: time, date, duration of interaction, focal monkeys' I.D., general location, activity, number of individuals within range of the interaction, and a brief description of the interaction itself.

3.4.1. Identifying Targets

Ninety agonistic interactions in total were of sufficient quality to be analysed in detail using a modified version of EWMN. Measures included duration of various postures held, distance travelled by each individual, direction (relative orientation between partners), opposition (closest body part between partners) and relative distance between opponents. ELAN, an annotation program, was used to score and notate the videos. See Chapter 2 for more details. Of these, 34 were considered to be high-intensity interactions, meaning they contained symmetrical and asymmetrical aggression, in which both males participated either in a defensive and/ or offensive fashion, as well as interactions in which only one male exerted aggression (such as a chase scenario). Of these 34, ten interactions included one or more hits, meaning that an individual either directed or made contact with their opponent using their forearm or teeth. These interactions were assessed separately on a frame-by-frame basis in slow-motion to identify target location. A hit was scored when contact was made with the opponent's body, as well as in cases where the attacker was clearly lunging at a specific body target. (following Reinhart 2008 p. 29). Hits were categorized according to location on the body as follows: Body/Torso; Forelimbs; Head/Neck/Shoulder; Hind limbs. In addition, measures of postural changes, relative opposition scores, and relative distance between opponents were used to construct a qualitative description of fights and sequences of high aggression, and also to test hypotheses concerning male tactics (See Chapter 2 for more details). Sample sizes vary slightly depending on analyses.

3.4.2. Wound Counts

During both 2009 and 2010, general information on wounds for both males and females (I.D., date, location on body and severity of wound) was collected by all researchers working at Samara (Nicola Forshaw, Petra McDougall, Dave McCaffrey and myself in 2009; Graham Pasternak, Natalie Freeman, Ria Boner, Tricia Rubi and myself in 2010). From these data, wounds were categorized in the same fashion as hits, i.e., according to location on the body as follows: Torso/Tail; Forelimbs; Head/Neck/Shoulder; Hind limbs. Wound location counts were also compared quantitatively between males and females for the Samara vervets, and also to hit counts on the body for males.

3.5. Results

3.5.1. Wound Location

A total of 110 wounds were recorded at Samara. These did not occur at random ($X^2 = 27.7$, df= 3, $p < 0.001$), but occurred in higher proportions on the body/tail (45%), as well as the head/ neck/ shoulder region (27%) (Figure 3.1).

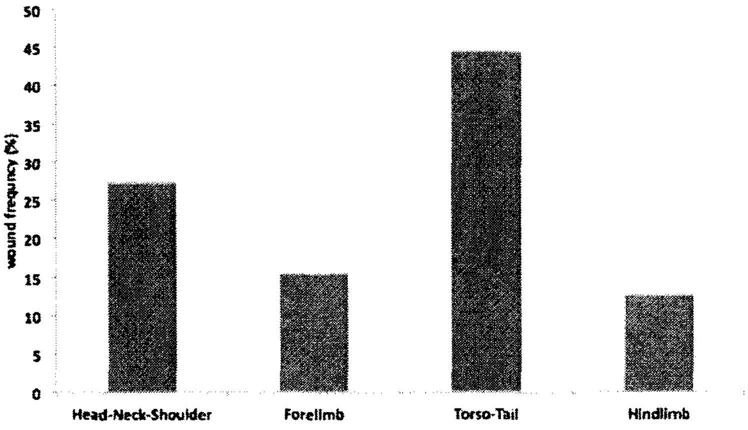

Figure 3.1. Wound frequency by body location for Samara vervets ($N_{wounds} = 110$).

When the data were partitioned by sex, however, male wound frequency diverged from this general pattern, revealing a higher proportion of wounds on the head/neck/shoulder region and the forearms compared to females (Figure 3.2. $X^2 = 16.8$, df= 3, $p < 0.001$; males N= 73 wounds; females = 37 wounds). Wounds were also calculated by randomly selecting a wound per individual in order to negate the possibility of one highly wounded individual biasing the data (Figure 3.3, males N= 23 wounds; females = 20 wounds). This confirmed the pattern in the group data.

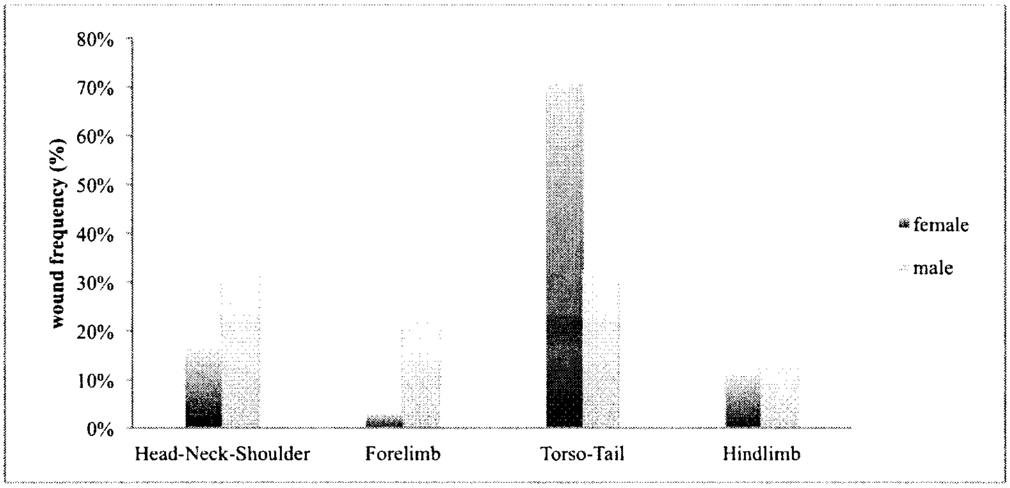

Figure 3.2. Wound frequency (%) by body location for male and female vervet monkeys at Samara ($N_{males} = 73$; $N_{females} = 37$).

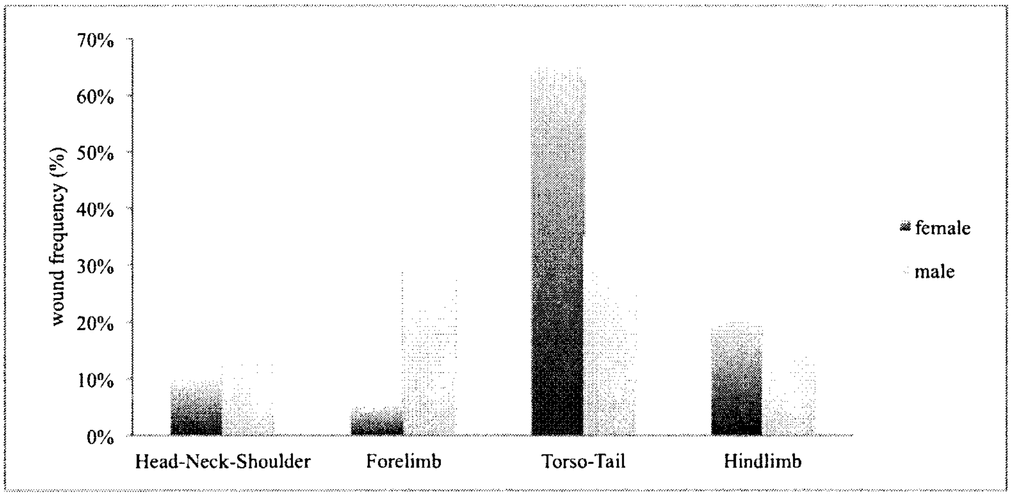

Figure 3.3. Wound frequency (%) per individual by body location for male and female vervet monkeys at Samara ($N_{males} = 23$; $N_{females} = 20$).

3.5.2. Confirmation of Targets

As noted above, ten interactions included actual hits, with 18 hits recorded in total. The majority of hits targeted the H/N/S region (n = 13, 72%), with the remaining hits targeted at the torso and tail region (n = 5, 18%). There were no hits recorded to the fore- or hindlimbs (Figure 3.4). Hit locations were not randomly distributed across the body ($X^2 = 25.1$, df = 3, $p < 0.001$), although this result should be treated with caution as some expected values were slightly below five in this analysis. Combining the data to form two categories of hits to the anterior region of the body (head-neck-shoulder and forelimbs) versus the posterior region (torso-tail and hindlimbs) produced a marginally significant result ($X^2 = 3.56$, df = 1, $p < 0.059$).

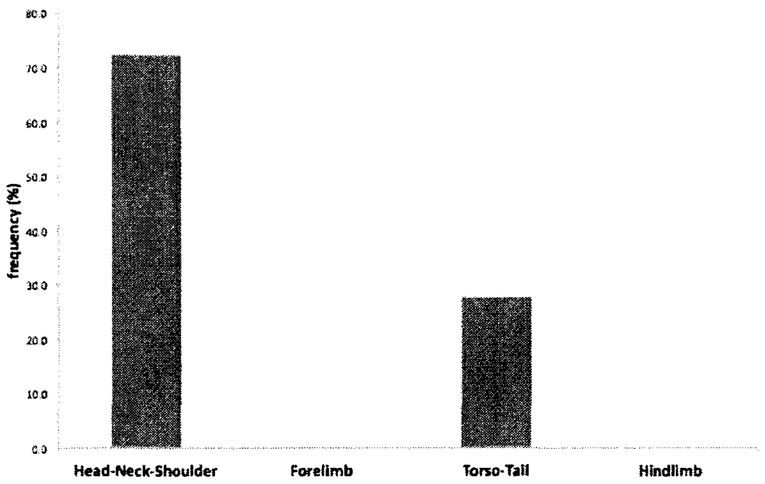

Figure 3.4. Percentage distribution of hits across body locations for male vervets (N = 18).

In order to compare the distribution of hits to wounds, the data were again combined into two categories of anterior and posterior body regions due to small sample size and expected values falling below five. The frequency distribution of hits did not did not differ significantly from that of wounds (Figure 3.5. $X^2 = 1.80$, df = 1, $p = 0.179$).

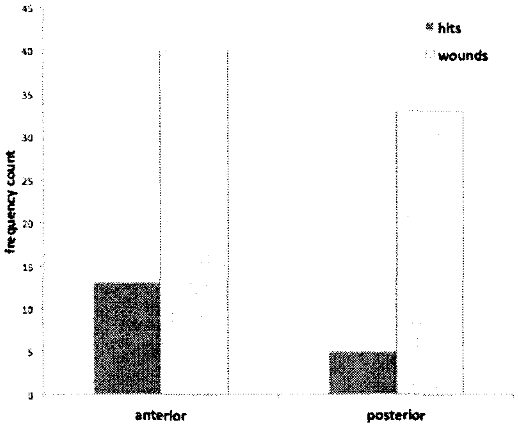

Figure 3.5. Frequency distribution of hits (N =18) and wounds (N =73) to the anterior and posterior regions of the body for male vervets.

3.5.3. Description of High Intensity Aggressive Encounters

For those interactions in which males ended up chasing each other in an overtly aggressive manner (i.e., not 'false chases': Henzi, 1985), but no contact aggression occurred, the most common response to an approach was for the opponent to adopt either a standing (11/23) or sitting posture (11/23 cases). In the remaining case, the male responded to the other's approach by immediately adopting a bipedal stance. Once males were in proximity, an average of two threat behaviours, as defined by Struhsaker (1967b) and Henzi (1982), were exchanged before a chase occurred. In total, 90 threats were exchanged during 21 of these encounters: 46% were solely eye-lid flashes, 23% involved headbobs with or without eyelid flashes, and in 31% males adopted a bipedal stance with or without eyelid flashes. In two cases, interactions did not appear to involve threat displays before chases occurred. During these interactions, one male approached the other with increasing speed and, once in close proximity (~5 monkey lengths), the male being approached ran in the opposite direction. It was unclear whether the male chasing intended to attack.

For interactions in which actual physical contact occurred, all but one involved some form of threat behaviour prior to the chase and/or strike. Twenty-two threats in total were exchanged (36% eye-lid flashes; 32% headbobs and 32% bipedal). In the one interaction that did not involve any form of threat display, the males were already in close proximity (1-3 monkey lengths) when filming began. Before the altercation occurred, Male JI placed his hand on the head of Male ED who offered submissive vocalizations in response; JI then groomed Male ED before moving off. Upon a second approach, Male JI immediately chased and exchanged blows with ED, who defended and counter-attacked before fleeing. Twelve of the males involved in fight interactions adopted a bipedal stance when striking their opponent, with three males standing quadrupedally and three males adopting a sitting posture. A total of 18 physical strikes were recorded across 10 interactions. Strikes were exchanged in only two of the interactions. A mean of 1.8 blows were struck per interaction, with a maximum of four blows struck in a single interaction. On average, the first blow was struck 4.2 seconds after the interaction began. In six cases, a strike brought the interaction to an end, with the attacked male either fleeing from the opponent (3/6 cases) threatening back and continuing to exchange threats without hitting before one of the males sat (2/6 cases) or by the opponent sitting (1/6 cases). In the remaining four cases, the male struck more than once before the opponent fled (2/4) or the opponent struck back (2/4).

More generally, during encounters that involved physical aggression, opponents adopted an "anti-parallel" or face-to-face position. In the majority of such encounters, one male lunged at the other, removing its forearms from the ground and attempting to attack with teeth and front limbs (70% of cases). Seventeen percent involved males in a sit-hind posture, again with forelimbs off the ground; in the remaining 13% of cases, the male launched a successful attack from a quadrupedal stance.

Individuals under attack generally responded by adopting either a standing posture, or jumping back from their opponent, twisting or spinning, so removing the target areas beyond the reach of the attacker. Males would also attempt to bite or swat their opponent in retaliation. When doing so, males would attempt to maintain a face-to-face orientation, and adopt either a bipedal posture or a sit-hind posture, both of which leave the arms free either to defend against further attack (by blocking a strike by the opponent) or to launch one of their own, while simultaneously restricting the initiator's ability to reach the assumed target (H/N/S). Males would also adopt a sit-haunch position in response to hits, in which the forequarters remain on the ground. This allows the animal to block access to sensitive areas such as stomach, groin and reproductive organs, while maintaining eye-contact with the opponent, and permitting tracking of their movements. Dropping down into a sit-haunch posture also serves to remove the target region away from the attacker, especially if the opponent is standing bipedally. A crouch posture was also seen under such circumstances, which can be viewed as a more extreme version of the sit-haunch posture, providing even better protection to sensitive regions of the body. Such postures are more obviously defensive than bipedal, sit-hind or standing postures, and they may also signal submission; sitting haunch ended three of the interactions in which a single blow was struck. Having said this, it is also true that tracking of the opponent occurred in all situations that males adopted a sit-haunch posture. It is possible, therefore, that a sit-haunch posture could be a counter-tactic, leaving the individual protected but capable of launching its own attack. Finally, males would sometimes flee from an attacker altogether, especially if successful bites and swats were taking place. Under such conditions, males would often receive further blows to the tail and hindquarters. Indeed, all such wounds seen on the tail in this study were incurred in this fashion.

3.5.4. Tactics used during High Intensity Aggressive Encounters

As noted above, during high intensity encounters, males would monitor each other continuously and attempt to strike from a face-to-face position. To quantify this, for each encounter, I combined opposition and direction scores in a manner that allowed me to calculate the duration that males spent in each of three orientations relative to each other: anterior-anterior, A-A (males maintain a face-to-face position); anterior-posterior, A-P (one male is oriented toward the other male's haunches from behind); anterior-side, A-S (one male is oriented toward the others male's torso and or haunches from the side, i.e. is oriented at a 90^0 angle). Males spent significantly longer in an A-A orientation than either an A-P orientation (matched pairs t-test: $t_{33} = -1.71$, $p = 0.048$) or A-S orientation

($t_{33} = -3.12$, $p = 0.002$), and they spent significantly longer in an A-P orientation than an A-S orientation ($t_{33} = -4.12$, $p = 0.0001$) (Figure 3.6).

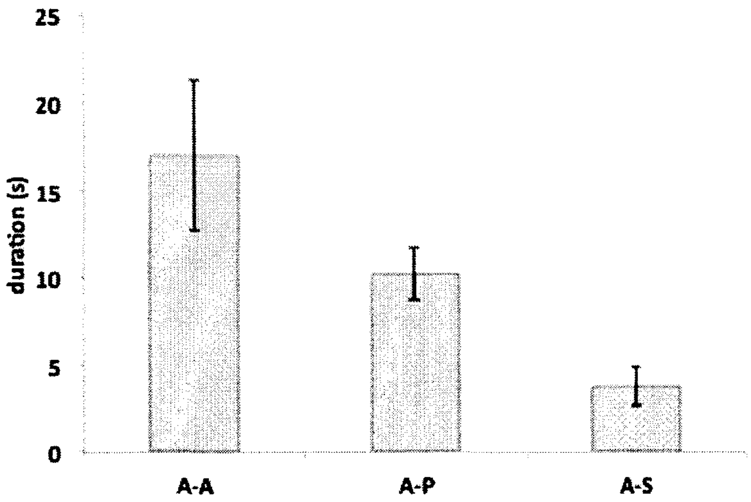

Figure 3.6. Duration (s) spent in Anterior-Anterior, Anterior-Posterior and Anterior-Side orientation during high intensity aggressive encounters (N =34). Bars represent means +/- 1 standard error.

Also as noted above, males appear to use certain postures, such as crouching or sit-haunch, in a defensive manner, serving to protect more vulnerable regions of the body, like the stomach and genitalia. Given this, I tested the prediction that lower ranking males would be more likely to adopt such postures during aggressive encounters and/or that they would hold them for longer durations. I assigned an ordinal rank to the males in each dyadic encounter (i.e., scoring the higher ranking male as 1, and the lower ranking male as 2) and calculated the overall frequency with which each male adopted a given posture (it should be noted that, in this analysis, some males are represented more than once, but as these were distributed equally over higher and lower ranking positions, this should not introduce any systematic error; nevertheless, the results should be treated with some caution).

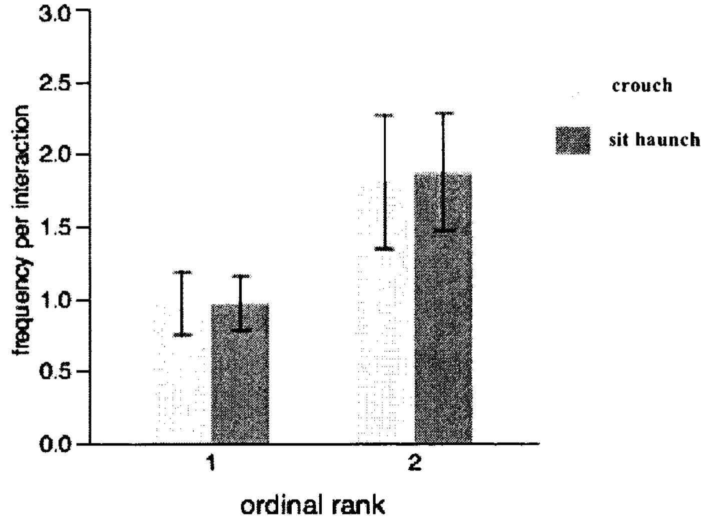

Figure 3.7. Frequency with which crouch and sit-haunch postures were adopted by males holding the relatively higher-ranking position in an interaction (ordinal rank = 1) versus males occupying the lower-ranking position (ordinal rank = 2) males. Bars represent means +/- 1 standard error.

Males in the lower-ranking position adopted the more defensive crouch and sit-haunch postures significantly more frequently than males in the higher-ranking position (Fig. 3.7. Crouch: $t_{58} = 1.64$, $p = 0.05$; sit-haunch: $t_{58} = 2.03$, $p = 0.02$), whereas there was no significant difference in the adoption of more offensive attacking postures like bipedal standing and sit-hind (Fig 3.8. Bipedal: $t_{58} = 1.06$, ns; sit-hind: $t_{58} = 0.57$, ns).

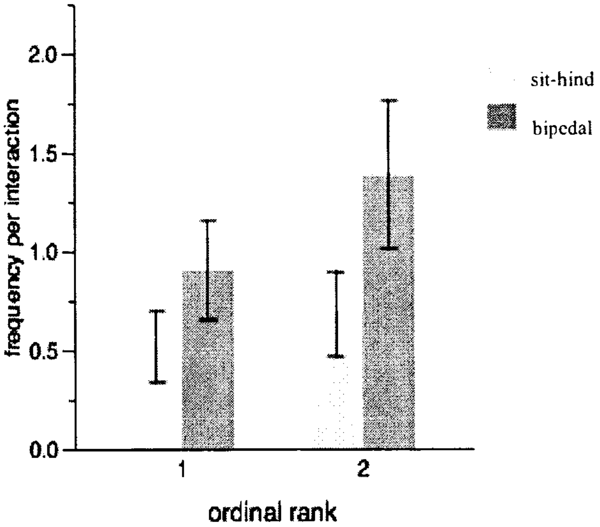

Figure 3.8. Frequency with which sit-hind and bipedal postures were adopted by males holding the relatively higher-ranking position in an interaction (ordinal rank = 1) versus males occupying the lower-ranking position (ordinal rank = 2) males. Bars represent means +/- 1 standard error.

Similarly, if we consider the duration for which such postures were held (calculated as the total length of time that males spent in a given posture over the course of an interaction), males in the relatively lower-ranking position maintained the sit-haunch posture for longer than males in the higher-ranking position (Figure 3.9. Sit-haunch: $t_{58} = 1.93$, $p = 0.05$; Crouch: $t_{58} = 2.29$, $p = 0.02$), whereas there was no difference for either sit-hind or bipedal postures (Figure 3.10: Sit-hind: $t_{58} = -0.63$, n.s.; Bipedal: $t_{58} = 0.46$, n.s.).

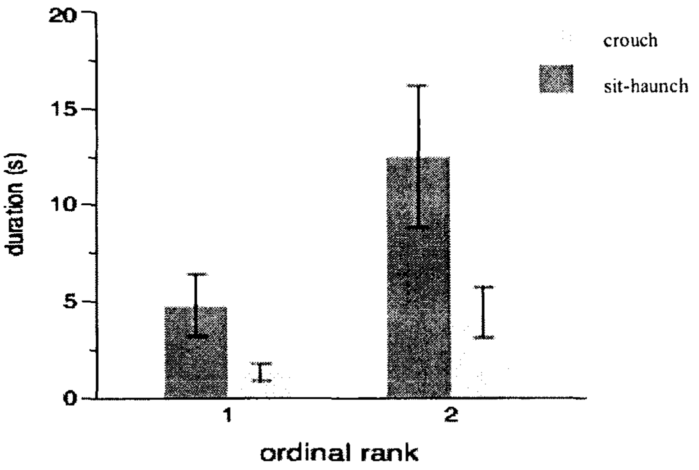

Figure 3.9. Duration that crouch and sit-haunch postures were held by males in the relatively higher ranking position in an interaction (ordinal rank = 1) versus males occupying the lower-ranking position (ordinal rank = 2) males. Bars represent means +/- 1 standard error.

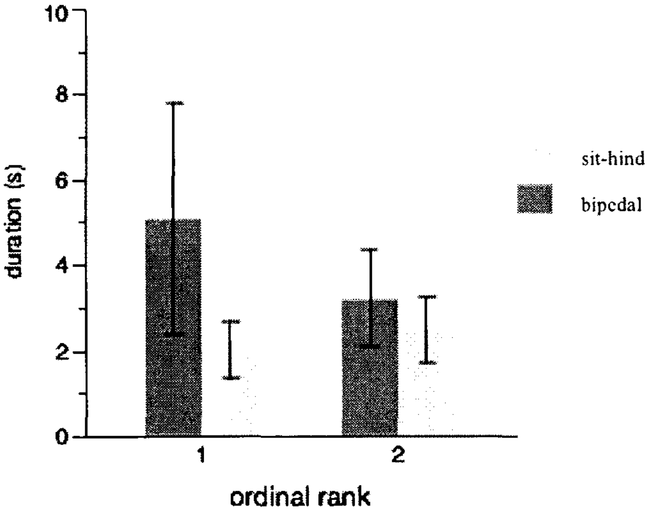

Figure 3.10. Duration that sit-hind and bipedal postures were held by males in the relatively higher ranking position in an interaction (ordinal rank = 1) versus males occupying the lower-ranking position (ordinal rank = 2) males. Bars represent means +/- 1 standard error.

3.5.5. Contextual Factors Influencing the Occurrence of High Intensity Aggression

Male Rank: Using the full dataset, I investigated whether male rank (in the form of normalized David Scores) was a predictor of whether an interaction escalated into high-intensity aggression. Specifically, I considered whether the rank distance between opponents predicted whether interactions would involve either a chase and/or fight. To do so, I combined chases and fights into one category of high-intensity aggression (Level 1) and categorized all the remaining threat interactions as low-intensity aggression (Level 2). In this way, I was able to conduct an ordinal logistic regression, with a binomial probability distribution and logit link function. Level of intensity was entered as the dependent categorical variable, with normalized rank distance as a fixed effect, and Actor I.D. (i.e., the male who initiated the interaction) and Reactor I.D. as random effects. Rank distance was not a significant predictor of level of aggression (Fig. 3.11. Fixed effects: $F_{1,87} = 2.48$, n.s.).

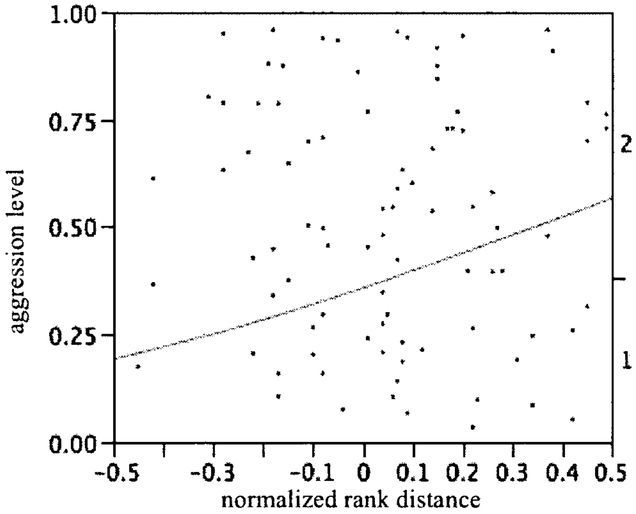

Figure 3.11. Normalized rank distance plotted against aggression level (1 = high-intensity aggression; 2 = low-intensity aggression). An ordinal logistic regression, with a binomial probability distribution and logit link function was conducted with level of intensity entered as the dependent categorical variable, normalized rank distance as a fixed effect, and Actor I.D. (i.e., the male who initiated the interaction) and Reactor I.D. as random effects.

Number of Males, Females and Habitat Type: An ordinal logistic regression on the full dataset revealed that there was also no significant effect of the number of other adult males in the vicinity, adult females or habitat location (woodland, bush and open ground) on the occurrence of escalated aggression (Full model: $X^2_4 = 5.48$, $p = 0.21$).

3.5.6. Male-Male Proximity Effects

Using the full dataset, I investigated the mean distance at which one male changed his posture in response to the approach of another male toward him was 2.71 monkey lengths (S.E. = +/- 0.17). There was no significant influence of aggression intensity on the distance at which a male adjusted his posture (Fig. 3.12: t_{88} = -0.3.76, n.s.).

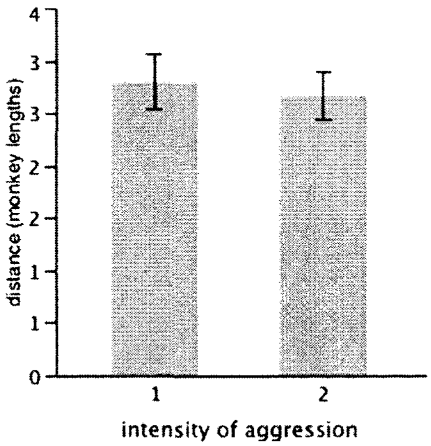

Figure 3.12. Distance (in monkey lengths) at which first change in posture occurred at the approach of another male. Bars represent means +/- 1 standard error.

Standard least squares regression was used to investigate whether there was any rank effect on the distance at which the first posture change took place, with rank distance (calculated from normalized David's scores) entered as a fixed effect, and actor I.D. and reactor I.D. entered as random effects. There was no significant effect of rank on the distance at which the first posture change occurred (Fig. 3.13. $F_{1,87} = 0.009$, n.s.).

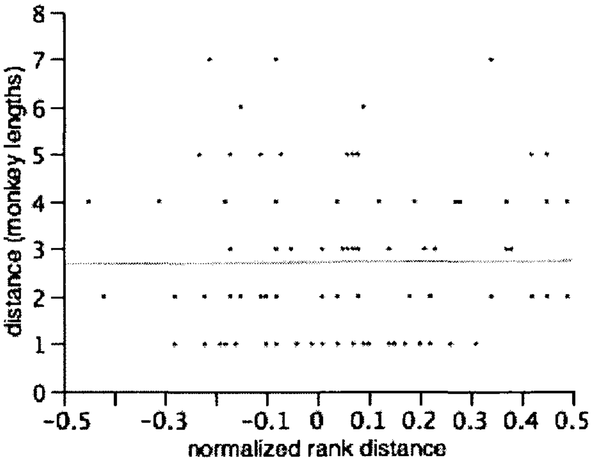

Figure 3.13. Normalized rank distance plotted against the distance (in monkey lengths) at which a male first changed posture on approach by another male. Standard least squares regression was used to investigate whether there was any rank effect on the distance at which the first posture change took place, with rank distance (calculated from normalized David's scores) entered as a fixed effect, and actor I.D. and reactor I.D. entered as random effects. There was no significant effect of rank on the distance at which the first posture change occurred.

3.6. Discussion

My results show that male vervets at Samara show a prevalence of wounds to the head, neck and shoulder, as well as the torso/tail regions. They also displayed wounds to the forearms and hindlimbs. This stands in contrast to previous reports of wounds in vervet monkeys, which documented that wounds occurred most frequently on the tail and hindquarters (Struhsaker, 1967b; Henzi 1982). Henzi (1982) also found that the pattern of wounding between males and females was almost identical, with the vast majority of wounds occurring on the hindlegs and tail, i.e., similar to the pattern shown by females at Samara. This suggests a difference in the mode of engagement shown by males across these studies. Wounds to the hindquarters of the body are most likely to be received when one animals turns tail and runs from its opponent, whereas wounds to the head, neck and shoulders occur when animals maintain a face-to-face orientation, and lunge toward each other. I also showed that, during actual fights, the majority of blows struck the head, neck and shoulder region, in clear preference to the posterior regions of the body (although the sample size was small, and should perhaps be treated somewhat cautiously).

If we assume that this pattern of actual hits is indeed representative of the Samara population, it suggests that Samara males are more likely to engage opponents in face to face combat compared to the animals studied by Struhsaker (1967b) and Henzi (1982). This could reflect enlarged group size and concomitant intensified competition for mates experienced by males in this population. As Freeman et al., (2012) documented (and I witnessed myself), there can be large influxes of new males into the troops during the mating season at Samara, which reduces the stability of the dominance hierarchy and intensifies competition over fertile females. Under such conditions, males may engage in many more bouts of active combat and, with higher benefits to be gained, may be prepared to stand their ground for longer, paying the relatively higher costs of engaging aggressively, rather than attempting to avoid aggression and retreating. Interestingly, Lawes and Henzi (1995) found a pattern of wounding similar to that of Samara males in a study of male samango monkeys (*Cercopithecus mitis*); a species that also experiences intense influxes of males into groups during the mating season. Lawes and Henzi (1995) suggested that the pattern seen in samangos reflected their social structure, which consists of one-male units. They argued that, as males usually do not co-reside in groups, except during the mating season, males lack the ability to negotiate social space with their competitors in any kind of non-aggressive ritualized form, and so end up engaging in potentially damaging fights. Given that vervet monkey males reside together year round, and clearly possess more ritualized displays, as documented comprehensively by Henzi (1981, 1985), it suggests that this explanation may not be the whole story for samangos, and may have more to do with male cohort size, competitive intensity and rank uncertainty between males. Such factors may lead males to more actively contest resources, rather than non-aggressively avoiding such competition, or using more formalized means to decide disputes. New males immigrating into a group represent an unknown quantity and may result in more aggressive challenges for rank than are seen among males that have been co-resident in a troop for a longer period. Larger cohorts of male may also inherently be more unstable. These possibilities could be tested by more systematic comparison of male cohorts of different sizes, both across different species, different groups of the same species, and across mating seasons within a group. It would also be interesting to determine whether there are any seasonal fluctuations in patterns of wounding; that is, whether during the non-mating season males are more likely to retreat from aggressive animals, risking bites to the rear rather than standing to engage in active combat.

Although a clear case can be made for the head, neck and shoulder as the primary target of male vervet monkeys (a pattern which also fits with that the closely related patas, as well as the samango), it is perhaps worth pointing out that attempting to bite or swipe the head area of an opponent places males at a high risk of receiving a wound of their own. That is, directing one's own weaponry toward the region of the opponent's body that sport the very same weaponry could be viewed as rather counter-productive, if we assume males are attempting to inflict the most damage with the least risk. (Of course, at least some biting and swiping movements made by males will be defensive, rather than offensive, aimed at warding off their opponent, but this doesn't detract from the fact that, when males go on the defensive they lunge towards their opponents' head and neck.) Given this, it seems possible that the head, neck and shoulder become targets because males may be highly motivated to protect more vulnerable areas of the body, like the genitalia, from attack. As the data showed, although males remained oriented in a face-to-face position for the majority of time during an interaction, they nevertheless achieved and maintained an anterior-posterior and anterior-side orientation at times. In addition, males were seen to adopt a crouching or sit-haunch posture that brought their body lower to the substrate, and obscured the genital region from view. The lower-ranking male in a given interaction was also significantly more likely to adopt such postures. As there are clear disadvantages to theses postures from an offensive perspective -- it would take longer for a male to get into position to strike a blow, and males may more readily telegraph their intention to strike from this kind of posture -- it seems unlikely that these can be viewed as attacking manoeuvres, and are best seen as defensive. Lower-ranking males are also known to adduct their testes into their body cavity during social encounters with higher-ranking males, and more dangerous/fear-inducing situations are more likely to lead to testis adduction in all males (Henzi, 1981), suggesting that males are sensitive to threats to the genital regions, and take action to prevent it. One possibility, then, is that males maintain a face-to-face orientation in order to keep their hindquarters out of the reach of their opponent's weaponry, and this results in the head, neck and shoulder region becoming the target area. That is, the hindquarters and genitalia represent the 'preferred' target, but lack of access to this area results in bites to non-preferred targets.

Certain aspects of the displays that high-ranking males perform around lower-ranking males support this interpretation, most notably, the 'red-white-and-blue' (RWB) display and the 'broadside', described by Henzi (1982). In the RWB display, one male circles around the other "confidently" (p.140), holding the tail aloft, and displaying the brightly coloured scrotum and extended, erect penis. The subordinate male also turns and circle around on his own axis in response to the displaying male, in order to keep the displaying male in view, and also ensure that his own genitalia are not exposed and vulnerable to attack. Henzi (1985) also reports that subordinate males in such a position often sit-haunch, and usually adduct their testes. In a broadside display, a more dominant male approaches a more subordinate male, and then turns to stand at 90° to it, often taking a few steps past, so that the erect penis and scrotum is highly visible to the subordinate. Again, this display leads subordinates to adopt more hunched postures and back away from the displaying male (Henzi, 1985).

From these descriptions, it is clear that males can engage in ways that do appear to be quite ritualized, and do not seem to represent a form of stalemate or dynamic equilibrium between males who are actually attempting to inflict wounds. Indeed, Henzi (1985) describes the subordinate males response to dominant males (particularly testes adduction) as 'homage'; a way for subordinate males to indicate and emphasize to dominant animals that the "relational 'rules'" (p. 144) of social engagement are being adhered to. By the same token, Henzi (1985) suggests that the displays of dominant males, which notably involve the erect penis (as well as abducted testes), function to 'teach' subordinates the significance of the signal, as the extended penis is highly correlated with the giving of aggression (Henzi, 1985). The bright colours of the genitalia, in this reading, may thus serve as 'amplifiers', increasing the detectability, memorability and discriminability of the display (Hebets & Papaj, 2005) (the fact that genital colouration alone cannot elicit appropriate responses from males, reported by Henzi (1985), supports this interpretation.) As Pellis (1997) has suggested, many forms of ritualized aggressive behaviour may be movements seconded from those used in combat; in the case of vervets, the heavy emphasis on the genitalia, with active display by dominant animals, and, in particular, the hiding and obscuring of the genitalia by subordinates, which mimics the tactics used in actual fights, suggests this could be true of vervets as well. As such, the genitalia may be more of a focus of aggression than the actual pattern of wounding and successful hits seen in this study would suggest. Henzi (1985) argues that scrotal and penile signalling likely evolved from preadaptations for sex. While this is no doubt true, it also seems possible that male combat tactics have played a role in determining the specific manner in which these signals are deployed.

Clearly, determining whether or not the genitalia or the head region represent the preferred target of vervet males requires further study. One way to test this would be to investigate more comprehensively the contexts and causes of wounding: do all tail and torso wounds arise as males are running away from their opponents, or do some occur when one male manages to evade the other's defences? Also, one could assess whether males work to maintain a face-to-face orientation because they are attempting to keep their opponent's face continually in the visual field (Powers, 1973), or whether they are attempting to manoeuvre around their opponent, while their opponent attempts to do the same, so that the face-to-face orientation arises as by-product of this jockeying for position. The fine-grained patterns by which males track and respond to the other's movements should reveal which of these is the case. For example, tracking opponent head position, and keeping the perception of the opponent's head stable, should produce smaller angular deviations from a central plane by the actor's body, whereas attempting to move around the opponent's defences and contact the posterior end of the body should result in larger angular deviations. Investigation specifically of genital signalling by Samara males would also pay dividends, both to assess whether Henzi's findings that adduction is associated only with subordinate males in social situations, and that penile extension is associated with aggression, are also true for the Samara population, and also to investigate how genital signalling is linked to both combat and threat displays more generally.

With respect to determining factors that influence the likelihood of escalated aggression, I found no relationship between intensity of aggression and the distance at which one male responded to the approach of another, suggesting that males probably do not approach others in ways that give off cues about aggressive intent. This may be because such cues are not possible (which seems unlikely, given that studies of humans have shown that emotions are discriminable from gait e.g., Dittrich, Troscianko, Lea & Morgan, 1996; Alaerts, Nackearts, Meyns, Swinnen & Wenderoth, 2011) or because males do not give off any such cues because they do not approach other males with any such intentions; rather these arise in the course of the interaction. What I did find, however, was that males began to mount an active response to another only once the male had approached to within 2-3 monkey lengths. This suggests that Szamado's (2008) predictions regarding proximity as an influence on threat displays is worth considering in more detail, and I pursue this further in the next chapter.

My results also showed that rank distance between two males was not a predictor of the level of aggression seen in an interaction, nor was rank distance a predictor of the distance at which a male would respond to the approach of another. Interestingly, when I initially ran the analysis on aggression level without including random effects, the effect was significant, but this vanished completely once male identity had been accounted for. While this was not due to the over-representation of a single male in the dataset, it does suggest that individual differences between males have a large influence on how an encounter develops. That is, rank is only one facet of a male's identity or personality, for want of a better term, and does not capture the experiential factors that might lead males to respond differently to circumstance. Such experiential factors can be long-term (such as developmental history, and previous social experience, e.g., Strum 1983), but may also reflect short-term experiences, such as previous encounters with particular males, occurrence of inter-group and territorial encounters, recent mating success, health status (including presence of wounds), all of which will influence the males emotional state, and hence threshold for engaging in certain forms of behaviour. Of course, this is precisely what Griffiths and Scarantino (2005) mean when they say that emotions and behaviour are situated. Understanding how situatedness influences male-male encounters may therefore require an additional, more systematic, form of data collection: focal samples conducted on males to record maintenance activities and social interactions in more detail, would give more context to their behaviour in social encounters than is possible with the semi-systematic approach to data collection used here.

Similarly, the lack of a relationship between habitat, number of other males present and number of females present during an interaction on the level of aggression displayed does not mean that contextual factors do not play a role in male-male encounters, only that the measures used here may have been too crude and lacking the necessary resolution. For example, the number of other animals present was scored from the video and may not be an accurate count of the number of animals present in the vicinity that could influence male behaviour; perhaps males are also sensitive to the identity of the animals present, to animals they can hear and not see, or to their relative position in the troop (centre versus periphery). Equally, the analysis itself may have been too crude: correlating gross contextual factors with the outcome of an interaction may miss many relevant features of the situation. Nevertheless, one has to start somewhere, and determining whether any obvious influences like habitat structure or presence of other individuals provides a good starting point: had any of these shown a significant relationship, it would have provided useful pointers as to where the analyses should then head. The lack of any such relationship is also useful, as it suggests a more refined approach may be needed, with more detailed data collected on context.

One other possibility, however, is that male-male interactions are simply not very predictable events. While particular contextual factors may predict the likelihood that an interaction of some kind occurs, its time course and outcome may not roll out in any predictable fashion because, being primates, males are not confined to any kind of classical 'signal-releaser' style interaction, as seen for example in amphibians, fish and insects. Instead, male interactions may be inherently protean, and contingent on moment by moment changes in male emotional state, which may reflect the current information it can pick up from its opponent.

In the next chapter, then, I investigate whether male-male agonistic interactions show any temporal predictability; specifically, whether the use of particular threat-related postures and facial expressions can predict the response shown by their social partner, and whether proximity influences the frequency and nature of threat displays in a manner consistent with Szamado's (2008) theoretical work.

CHAPTER FOUR:
PROXIMITY AND PREDICTABILITY

4.1. Introduction

Threat displays have attracted attention from evolutionary theorists over the years because they raise inherently interesting questions about their evolutionary stability (Maynard & Smith, 1973; Zahavi, 1975: Enquist, 1985; Hinde, 1985; Miller, 1997; Számadó, 2008). The function of a threat display is to reduce the probability of actual fighting taking place, and hence reduce the costs of incurring potentially damaging injury. Threat displays thus represent a means by which males can assess their respective RHPs and make decisions about whether or not they should escalate an encounter (Számadó, 2008). This means that, if threat displays work, then all individuals should use them. If, however, all individuals use them, then they no longer convey useful information (i.e., they are no longer reliable) because there appears to be nothing to prevent weak individuals from using such displays dishonestly (Számadó, 2008). That is, if threat display always prevent fighting from taking place, weaker males will be able to produce such displays as effectively as stronger individuals, and win encounters that they would otherwise lose if an actual fight were to take place.

Zahavi (1975, 1977) therefore suggested that threat displays would need to be costly to be reliable (i.e., they would function as handicaps), such that the costs of producing them would be disproportionately high for weak individuals, and only individuals who could bear these costs would produce such signals, thus ensuring reliability. Enquist (1985), however, formulated a model to show that cost-free signalling could evolve provided certain key conditions were met, and argued that it was the *potential* costs of having to fight against a stronger individual that kept displays honest, and hence evolutionarily stable. Számadó (2003, 2008) has pointed out that Enquist (1985) left unanswered the question of where this potential cost came from. Számadó's (2003) solution was to suggest that the cost of threat displays was inherent to the situation in which individuals found themselves. That is, signal reliability/honesty is maintained by the inherent risk of threatening an individual that might be willing to retaliate and fight back. Taking this further, Számadó (2008) suggested that it was "proximity risk" that ensured reliability. More specifically, he suggested that threat displays are only credible within a certain distance of the opponent, and that this threshold distance is strongly related to the weaponry and species-specific fighting techniques. As such, honest signalling is only an EES within a certain distance from the opponent (Számadó, 2008) – the "honest striking" distance. Outside of this zone, signals may be a mixture of honest and dishonest signalling – the "dishonest striking distance"—and outside this zone, signals are unreliable and should not be used. In other words, the function of a threat display is to convey information about the risk of an impending attack, i.e., the displaying individuals willingness to fight.

As discussed more fully in Chapter One, theorists have also argued that threat displays cannot be interpreted as such until the animal at which they are directed has made a response; a threat only becomes a threat once the other animal has behaved in a manner suggesting that the behaviour was seen as threatening (i.e., by escalating the interaction, by fleeing the interaction, by adopting postures that protect vulnerable body parts etc). Hinde (1985) and Griffiths and Scarantino (2005) have argued that not all "threat displays" are driven by the need for one animal to display its RHP to another in a competitive situation; rather, one animal may be in a state of uncertainty regarding another's motivation/emotional state, and so it 'throws something out into the world", behaviourally speaking, in order to provoke a response and acquire more information about how it should continue to act. In this way, threats displays and aggressive interactions are emergent properties of an ongoing situation, and do not necessarily reflect the execution of a pre-exisiting intention to attack in the head of one, or both, of the males. In other words, not all "threat displays" produced by males are necessarily threat displays in the sense used by Számadó (2008); rather, they are behaviours by which males can acquire further information about the nature of the situation in which the male finds himself, and so decide how to behave. This suggests that the use of threat displays may be more variable than Számadó (2008) implies, and that interactions need not follow a set 'ritualized' pattern, in which the actions of one male trigger a specific kind of response in the other. Male-male threat interactions of the kind recorded here may well be of this unpredictable nature, given that, as already discussed, male vervets do possess certain kinds of ritualized behaviours that appear to function as a way for males to recognize and acknowledge their relative ranks. That is, males appear willing and able to use ritualized behaviour on some but not all occasions. Threat displays of the kind studied here, that do not involve any heavily ritualized elements, might therefore be expected to be much less predictable because they are, in essence, information-seeking exercises.

In the previous chapter, I identified the targets and tactics used by vervet males during high-aggression encounters, and showed that contextual factors, such as the number of females or other males present, and male dominance rank, had no influence on their outcome. I also suggested that the reason for the latter finding was that male-male aggressive interactions are not particularly predictable events. Building on this, and incorporating the theoretical insights of Számadó (2008), Hinde (1985) and Griffiths & Scarantino (2005), my aims in this chapter are (a) to test the prediction that vervet monkeys should have a low distance threshold for the 'honest striking distance', given their use of teeth and hands as weaponry, and the nature of the tactics used in fights and (b) to test whether male threat interactions show any evidence of being ritualized; that is, whether the behaviour of each male is dependent on that of the other throughout the sequence of interaction. More specifically, I test the predictions that (i) the production of threat displays should peak at a distance of 1-2 monkey lengths and decline with increasing distance between opponents; (ii) that this pattern can be broken down by the nature of the threat display used; specifically, that bipedal bobs, which place a male in a striking posture and indicate willingness to fight, should peak at the closest distances and drop off quickly, whereas those threats that do not involve the presentation of weaponry to the same degree – specifically eyelid flashes and head-bobs – should occur at a lower frequency at the closest proximity, and a higher frequency at longer distances. That is, the threat display curve will arise because of differential performance of different kinds of threats at different distances; (iii) that, as males target the head/neck/shoulder region, and spend significantly longer holding a face-to face orientation during high-intensity aggressive interactions, males should also be more likely to produce threats while in a face-to-face orientation, as another means of indicating their willingness to fight, and that this should also vary with distance; and (iv) that male threat displays will show no evidence for ritualization; instead threat interactions will show evidence indicating that males are 'prospecting' or seeking further information about their competitors.

4.2. Methods

Two habituated troops of vervet monkeys (RST and RBM) were followed during two mating seasons (April through July 2009/ 2010) and interactions between males were video taped using a semi-systematic focal sampling procedure (see Chapter 2 for details). All videos were compiled into a database and general information about the interaction was recorded: time, date, duration of interaction, focal monkeys' I.D., general location, activity, number of individuals within range of the interaction, and a brief description of the interaction itself.

4.2.1. Characterizing and Scoring Threat Behaviours

Ninety agonistic interactions in total were of sufficient quality to be analysed in detail using a modified version of EWMN, with 87 containing threat behaviours that could be analysed for the purpose of this chapter. Measures included frequency of various postures held, direction (relative orientation of partners), opposition (closest body part between partners) and relative distance between opponents. ELAN, an annotation program, was used to score and notate the videos. See Chapter 2 for more details.

Threat behaviours were divided into three broad categories of eyelid flashes, head-bobs, and bipedal bobbing threats. These categories were based on those identified in previous studies (Struhsaker, 1967b; Henzi, 1982; Fedigan & Fedigan, 1988), and considered the most practical means by which to apply Számadó's (2008) model, as these provide an ordinal scale of threat intensity. Eye-lid threats are considered the least intense form of threat, head-bobs are intermediate and bipedal bob displays are considered most intense, as these place the animal in a position where its weaponry is on display, and willingness to attack is indicated (given the findings in the previous chapter where 70% of all successful strikes against an opponent took place from a bipedal position). Video-taped interactions were scored according to the sequencing of these behaviours, along with sit and stand postures and tabulated accordingly for analysis. For ease of computation, sit postures included sit-hind, sit-haunch and crouch as one category of defensive posture. Behaviours were recorded by intensity of threat and, if there was no threat, by posture. This meant that when behaviours occurred at the same time (i.e. eyelid flash and stand posture or bipedal and eyelid flash) only the threat behavior was recorded in each case, and not the posture as well. Analyses of information and entropy measures, and long-range correlations were conducted with the assistance of Dr. David Lusseau, University of Aberdeen, using code written in Visual Basic. Long-range correlations were calculated using a dedicated code in R written by Dr Lusseau (see appendix 1).

4.2.2. Information measures & Conditional Entropy

The information content of state sequences performed by two actors can be inferred from the transition probabilities (*p*) between states, under the assumption of different orders in the sequences (0-order, 1st order, and 2nd order). Here, the individual initiating the sequence will be labelled as the "Actor" and the other individual involved in the interaction will be labelled as the "Reactor". Entropic measure of information content (i.e., measures of uncertainty) can be derived from these sequences using Shannon's information theory (Shannon, 1948; See Barrett et al., 2012 for an application of this to behavioural interactions). It should be noted that the use of the word 'information' should not be taken to mean "knowledge", as we usually understand it, but rather the number of possibilities that can maximally exist; that is, in everyday language, information places constraints on our choices (an 'informed choice' is one where we have been able to eliminate certain options), but in the information theory sense, information refers to the maximization of a number of choices (see Steinberg & Conant 1974; Hanser, Doyle, McCowan & Jenkins, 2004 for more details).

We can derive the Shannon entropy, H(x), contained in the emission rate of states (0-order) from a set *x* of behaviours (when *x* represents a set of *n* states and *y* a set of *m* states) as follows:

$$\mathrm{H(x)} = -\textstyle\sum_1^n p_i log_2\, p_i \qquad (1)$$

(in bits), where $p_i = \frac{a_i}{\sum_i a_i}$ and a_i is the number of times state *i* was observed. A bit, as formulated by Shannon & Weaver (1949), is a unit of information equivalent to the amount of information required to choose between two equally likely alternatives. A choice between four equally likely alternatives would require two bits of information, and a choice between n alternatives would require $\log_2 n$ bits. In a simple system, where all events are equally likely, the selection of one event requires $\log_2 n$ bits of information. With each bit of information received, there is a decrease in uncertainty about the event that occurred. As alternatives in the real world are usually not equally likely, the probabilities that each event will occur have to be taken into account, which give rise to equation (1) above. In a system where one possibility is much more likely than any other, H(x) will be lower than in a system where events are more equiprobable, and in a system where an actor always sends the same message, there will be no uncertainty about what the actor will do, hence no information is transferred and so H(x) = 0. In other words, the more choices there are, the more uncertainty there will be about which one will be chosen, and therefore the more information will be conveyed with each signal (Steinberg & Conant 1974). H(x) is therefore a measure of diversity, and depends on the number of choices that are possible, and the way those choices are made (Steinberg & Conant, 1974).

The joint entropy of the sequence of states emitted by an actor and a receiver (1st order) can also be estimated:

$$H(x,y) = -\sum_{i,j} p_{ij}\, log_2\, p_{ij} \qquad (2)$$

where $p_{ij} = \frac{a_{ij}}{\sum_{ij} a_{ij}}$ and a_{ij} is the number of times state j was observed following state i.

This joint entropy measure can be used to estimate the conditional entropy, which in essence represents the ability to predict what a receiver will do given the behaviour of the actor:

$$H(y|x) = H(x,y) - H(x) \qquad (3)$$

As H(y|x) approaches zero, the following act is completely determined by the preceding one. In other words, there is no *information* contained in the transition between acts. We can then further assess the constraints placed on a succeeding act by the preceding one by estimating the transmission strength, *T*, normalised by the 'information' content of preceding acts, *t*:

$$T(x;y) = H(y) - H(x,y) + H(x) \qquad (4)$$

and $t(x;y) = \frac{H(y)-H(x,y)+H(x)}{H(y)}$ (5)

This ratio (i.e., $\frac{T(x;y)}{H(y)}$) will give a value of 0 if the immediate subsequent actions of the two animals are statistically independent of each other. The closer the ratio approaches 1 (i.e., as the value for T(x;y) approaches the value for H(y)), the more likely it is that the act of y is determined by the preceding action of x. Thus, the amount by which this value exceeds 0 and approaches H(y) is a measure of the constraint placed on the actions of one animal by the immediately preceding actions of the other (Steinberg & Conant 1974).

Finally, it is possible to estimate the amount of information the receiver receives when the actor performs a particular act, *J*, from:

$$T(x;y) = \sum_i p_i J(i;y) \qquad (6)$$

Hence, we can calculate the signal strength of each act by normalising this information to how often the act is performed, using the following equation:

$$p_i J(i;y) = \sum_j p_{j|i} \frac{p_{j|i}}{p_j} \qquad (7)$$

where $p_{j|i} = \frac{p_{ij}}{p_i}$.

These notions can then be extended to estimate the information value of 2nd-order assumptions on the act sequences (the actor influences the receiver who in turn influences the actor). We define first x_2 as the set of *k* states the actor can perform following the receiver to give:

$$H(x_2) = -\sum_1^n p_k log_2 p_k \qquad (8)$$

The resulting joint entropy is then given by:

$$H(x, y, x_2) = -\sum_{i,j,k} p_{ijk} log_2 p_{ijk} \qquad (9)$$

where $p_{ijk} = \frac{a_{ij}k}{\sum_{ijk} a_{ijk}}$

And the transmission of x_2 given that y and x was performed first is given by:

$$t(x, y; x_2) = \frac{H(x,y) - H(x,y,x_2) + H(x_2)}{H(x_2)} \qquad (10)$$

4.2.3. Long-term correlations

Following the method of Ferrer and Lusseau (2006), S = {si,...,sj,...,sn} can be defined as the set of behaviours we wish to analyse, where n = 6 in our vervets for the purposes of this analysis (i.e., directed approach; eye-lid flash; head-bob; bipedal stance; sit; stand: see Table 4.1). *Nij(d)* and *pij(d)* are defined as the number of times and the proportion of times, respectively, that the behaviour, *s*i, has appeared at temporal distance *d* before the behaviour, *sj*, within our collection of sequences. The temporal distance is defined in terms of position in the sequence of behaviours, i.e., each behaviour can be considered as a time step in the sequence. This gives:

$$p_{ij}(d) = \frac{N_{ij}(d)}{\Sigma_{si,sj \in S} N_{ij}(d)} \quad (10)$$

$p_i^-(d)$ and $p_i^+(d)$ are defined, respectively, as the proportion of times that s_i has appeared at temporal distance, *d,* before and after any element of *S* in the collection of sequences. This gives:

$$p_i^-(d) = \Sigma_{sj \in S}\, p_{ij}\,(d) \quad (11)$$

and:

$$p_i^+(d) = \Sigma_{sj \in S}\, p_{ji}\,(d) \quad (12)$$

The information transfer between patterns at temporal distance *d* is defined as:

$$I(d) = \Sigma_{si,sj \in S}\, p_{ij}\,(d) \log \frac{p_{ij}(d)}{p_i^-(d)p_j^+(d)} \quad (13)$$

I(d) is therefore a measure of the correlation between behavioural patterns (i.e., recurring patterns in the sequence of behavioural events, and not a measure of the correlation between behavioural events themselves; these just provide the information for calculating the correlation seen between patterns: Ferrer and Lusseau, 2006). Rank distance between males was also included in the analysis to see if this had influence on information transfer. The observed patterns were then compared to the mean and 95% confidence intervals for 1000 randomly permuted versions of the data set (Ferrer and Lusseau, 2006).

4.3. Results

4.3.1. Threat Displays by Distance

The mean number of threat displays performed per interaction declined significantly with distance between opponents (Fig. 4.1. $r_s = -0.964$, $n = 7$, $p < 0.001$). Partitioning the data by threat type showed the same pattern of decline across all three threat categories (Fig. 4.2. a-c. Eyelid flash: $r_s = -0.929$, $n = 7$, $p < 0.001$; Head-bob: $r_s = - 0.964$, $n = 7$, $p < 0.001$; Bipedal: $- 0.982$, $n = 7$, $p < 0.001$). (Analyses were conducted on mean values using Spearman rank correlation with distance coded as an ordinal measure; non-independence of data points precluded ANOVA or regression on the full data set. The full data set was, however, used to generate the graphs to provide both mean and standard error values for illustrative purposes.)

Using the full dataset (excluding two high-intensity interactions that did not contain any threats) to compare the frequency of the different types of threat in very close proximity (i.e., one monkey length), I found no significant difference between eye-lid flashes and bipedal stance threats (matched pairs t-test: $t_{86} = 1.292$, ns), nor was there any difference between bipedal stance displays and head-bobs ($t_{86} = -0.725$, ns). There was, however, a significant difference between eye-lid flashes and head-bobs ($t_{86} = -2.295$, $p = 0.013$).

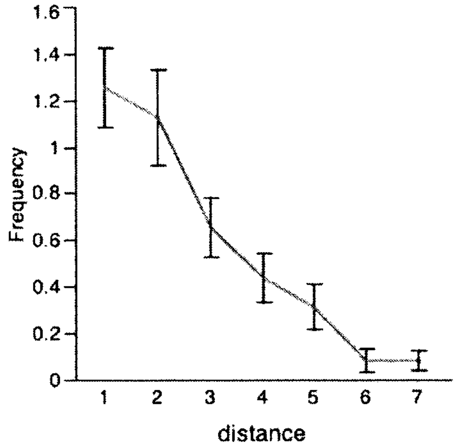

Figure 4.1. Mean frequency of threat behaviours (eyelid flashes; head-bobs; bipedal stance) plotted against proximity between opponents (measured in monkey lengths). Points represent mean +/- 1 S.E.

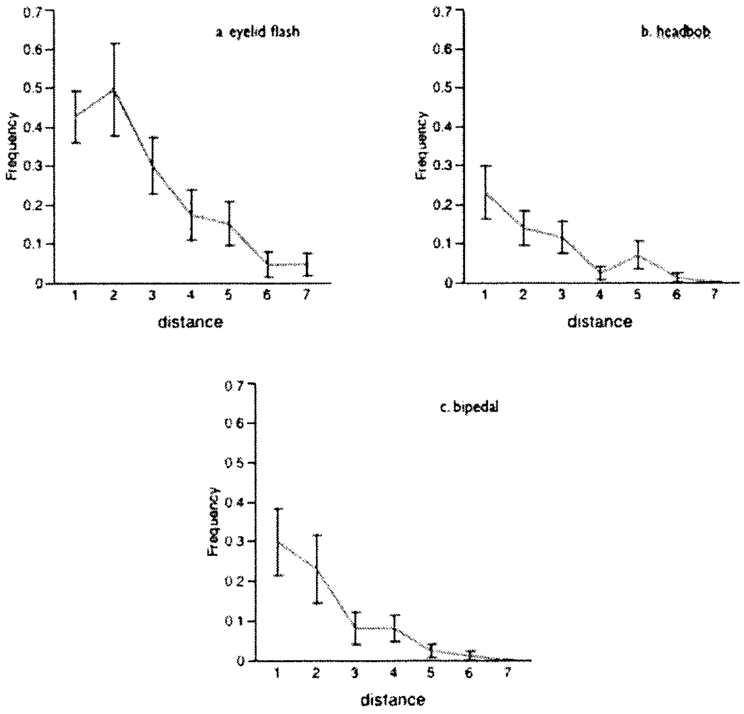

Figure 4.2. Mean frequency of (a) eyelid flashes (b) head-bobs and (c) bipedal stance threats plotted against proximity between opponents (measured in monkey lengths). Points represent mean +/- 1 S.E.

4.3.2. Threat Displays by Orientation

For the 56 interactions that contained no physical aggression or contact, males were significantly more likely to threaten their opponent while in a face-to-face orientation (anterior-anterior, A-A) than in either an anterior-posterior (A-P) orientation (matched pairs t-test: $t_{55} = -6.247$, $p < 0.0001$) or an anterior-side (A-S) orientation ($t_{55} = -4.963$, $p < 0.0001$), but there was no difference between threats oriented A-P compared to A-S ($t_{55} = 1.527$, ns) (Figure 4.3).

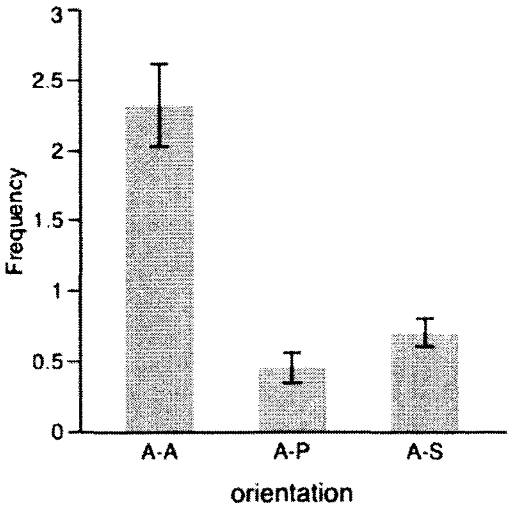

Figure 4.3. Frequency of threats produced by opponent in an anterior-anterior (face-to-face) orientation (AA), anterior-posterior orientation (A-P) and anterior-side (AS) orientation. Bars show mean +/- 1 S.E.

To investigate whether there was any effect of distance on the number of threats produced in each orientation, I created two categories "Close" (all threats occurring in 1-2 monkey lengths) and "Distant" (all threats occurring in 6-7 monkey lengths). In the close category, there was a significant difference in the number of threats produced in an A-A orientation compared to an A-P orientation ($t_{55} = -4.255$, $p < 0.0001$) and to an A-S orientation ($t_{55} = -3.629$, $p < 0.0003$) but no difference between an A-P and A-S orientation ($t_{55} = 0.903$, ns) (Figure 4.4a). By contrast, there was no significant difference in the number of threats across orientations for the distant category (A-A vs. AP: $t_{55} = -1.84$, ns; A-A vs. A-S: $t_{55} = -0.851$, ns; A-P vs. A-S: $t_{55} = 0.629$, ns) (Figure 4.4b).

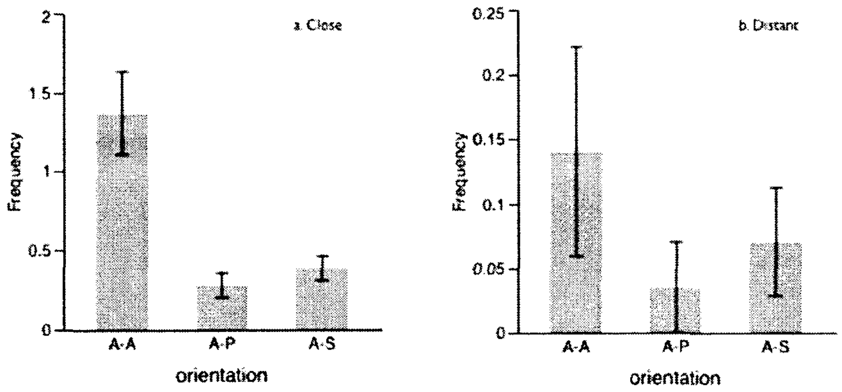

Figure 4.4. Frequency of threats produced by opponent in an anterior-anterior (face-to-face) orientation (AA), anterior-posterior orientation (A-P) and anterior-side (AS) orientation in (a) close proximity (1-2 monkey lengths) and (b) at a distance (6-7 monkey lengths). Bars show mean +/- 1 S.E. Note difference in the scale of the y-axis.

4.3.3. Information Measures and Signal Strength

Table 4.1 presents a summary of the behavioural sequences used for information and entropy analyses. Data show all 87 interactions scored by the first three moves in a sequence, i.e., Actor-Reactor-Actor. Full sequences of behaviour used in analyses are presented in Appendix 2. In total, 343 behavioural events were scored.

To begin, a 1st-order sequence analysis was run (actor-reactor). This revealed that the information content of the signal sent by the Actor, H(actor) = 1.89 bits, from a maximum of $\log_2(4) = 2$ bits. That is, the observed value is quite close to the maximum possible value, indicating a lot of information is transferred when the first individual acts. As inspection of Table 4.1 shows, the possible choices an actor can make are not all equally likely, but directed approaches, bipedal bobbing and eye-lid threats are all more likely than head-bobs, and occur at approximately the same frequency. In contrast, the information content of the signal sent by the reactor, H(reactor) = 2.065 bits, from a maximum of $\log_2(5) = 2.32$ bits. Thus, there is more uncertainty about what the reactor will do compared to the actor.

Following equations (2) to (6), the joint entropy, H(actor, reactor) was calculated, giving a value of 3.84 bits, which results in a conditional entropy value, H(actor|reactor), of H(actor, reactor) – H(actor) = (3.84-1.89) = 1.96 bits. That is, even when the initial act is known, there is a high level of uncertainty about what the next act will be (i.e., the value is not particularly close to zero). As noted above, the conditional entropy value permits an estimate to be made of normalized transmission strength, by calculating the ratio of T(actor;reactor) to H(reactor). T(actor;reactor) = H(reactor) + H(actor,reactor) – H(actor) = 2.065 – 3.84 + 1.89 = 0.115. This gives a value of T(actor;reactor)/H(reactor) = 0.115/2.065 = 0.0556 or 5.6%: very little information is transferred in each actor-reactor sequence, and hence there is a very small reduction in uncertainty. Calculating the value for 2nd order sequences (actor-reactor-actor) gave a value of 17.1% for transmission strength, which indicates a greater reduction in uncertainty compared to actor-reactor sequences, but still represents a rather weak signal (i.e., much closer to zero than to 1).

Table 4.1. Summary data of sequences of behavioural interactions of male vervet monkeys used for information and entropy analyses. Data show all 87 interactions scored by the first three moves in a sequence, i.e., Actor-Reactor-Actor's response. Full sequences of behaviour used in analyses are presented in Appendix 2. In total, 343 behavioural events were scored.

		ACTOR RESPONSE					
ACTOR	**REACTOR**	**BP**	**EF**	**HB**	**SIT**	**STD**	**TOTAL**
A*	**BP***	1	1	0	0	1	**3**
	EF*	0	0	0	1	9	**10**
	HB*	0	0	0	0	0	**0**
	SIT*	1	10	1	2	21	**35**
	STD*	8	16	1	0	14	**39**
BP	**BP**	6	1	0	1	7	**15**
	EF	1	0	0	1	15	**17**
	HB	0	0	0	0	5	**5**
	SIT	1	2	0	0	3	**6**
	STD	3	3	1	1	12	**20**
EF	**BP**	1	3	0	0	12	**16**
	EF	0	0	0	6	20	**16**
	HB	0	0	0	2	3	**5**
	SIT	1	4	5	5	25	**40**
	STD	7	10	7	9	22	**55**
HB	**BP**	1	1	0	1	4	**7**
	EF	0	0	0	3	6	**9**
	HB	0	0	0	2	5	**7**
	SIT	1	3	0	1	5	**10**
	STD	2	2	3	3	8	**18**
TOTAL		**34**	**56**	**18**	**38**	**197**	**343**

*A = approach; B = Bipedal; EF = Eyelid flash; HB = Head-bob; SIT = Sit; STD = Stand.

Table 4.2 presents the signal strengths calculated for individual signals sent by Actors and Reactors. For Actors, a directed approach represented the strongest signal, followed by a bipedal stance. Eyelid-flashes and head-bobs were much weaker signals than either of these two. That is, an actor approaching an opponent or adopting a bipedal stance (at any point in the interaction) had the greatest effect on reducing uncertainty about what the receiver would do next. For Reactors, the strongest signal was eyelid flashing – which represented a very strong signal relative to all the others – followed by adopting a standing posture. That is, the uncertainty surrounding what the Actor would do next based on the Reactor response was much greater for eyelid flashing than any other display produced by receivers. It should be noted that it is the pattern of values relative to each other that is important here, and not the absolute values of the signal strengths.

Table 4.2. Signal strengths for displays by Actors and Receivers.

I.D.	**BEHAVIOUR**	**SIGNAL STRENGTH**
ACTOR	**Approach**	**0.0515**
	Bipedal	0.0399
	Eyelid Flash	0.0018
	Head-Bob	0.0138
REACTOR	Bipedal	0.0224
	Eyelid Flash	**0.0855**
	Head-Bob	0.0283
	Sit	0.0114
	Stand	0.0330

4.3.4. Long-range correlations

Figure 4.5 shows the long-range correlations calculated for the 87 behavioural sequences that contained threat behaviours and could be scored completely from start to finish. More specifically, this shows the information content of the correlation between actor and receiver behaviour, that is, the dependency of what the receiver will do depending on the actor's behaviour. The x-axis represents the steps separating two events in the sequence (i.e., the actor's behaviour at time *t,* the reactor's behaviour at t+1, the actor's behaviour at t+2 etc), and the y-axis, *I(d)*, represents the information transfer across steps in bits. To interpret the graph, we look for the first step at which the observed information content (indicated by the open circles) falls to levels similar to what we would expect at random (indicated by the lines representing the mean and 95% confidence intervals calculated by randomly permuting the data). If threat interactions between males were ritualized and predictable, the graph would show a smooth decay of I(d) as the distance between steps increased, and these values would all be greater than chance. As is apparent, for vervet males, the graph does not show this pattern, and falls to random after only one step (i.e., this is the only this point falls outside the 95% confidence limits. The point that does so at around Step 35 represents a spurious correlation produced by boundary effects; that is, as we get to very long distances between steps, there are fewer data, and a greater possibility of significant correlations by chance.) In other words, the event correlation is only a single bit, and how males engage with each other is highly unpredictable following their initial engagement on the first step. There was no influence of rank distance on any correlation at any distance. In essence, then, males are throwing out behaviours with a certain probability, but the manner in which they do so is not predicted by the events that happened in the previous time step, bar the very first one.

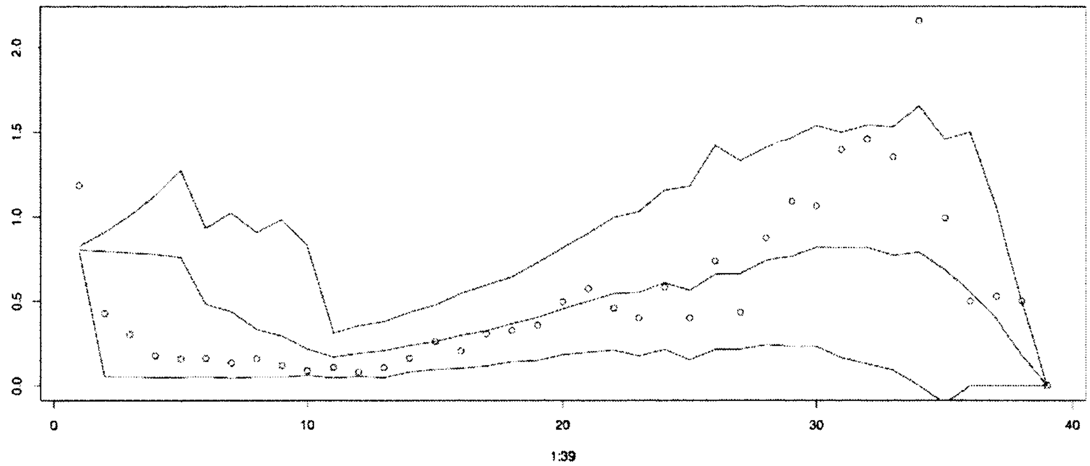

Figure 4.5. Long-range correlations calculated from sequences of male-male threat interactions. Sequence length (*x*-axis) runs from 1 to 39 steps, and I(d) (*y*-axis) is given in bits. Open circles represent observed data; solid lines represent the mean and 95% confidence intervals of 1000 randomly-permuted data sets. Analysis run by Dr David Lusseau, University of Aberdeen, using the R statistical package.

4.4. Discussion

My results show that (a) proximity risk influences the threat displays of male vervet monkeys but that (b) such threat displays appear not to be ritualized, and are largely unpredictable beyond males' initial engagement with each other.

All threat displays showed a decline with decreasing proximity between opponents, with a much higher frequency occurring at the closest distance of one to two monkey lengths. As predicted by Számadó (2008), then, proximity risk influences the production of threat displays. Interestingly, however, the prediction that the display signalling greatest willingness and readiness to fight, the bipedal bobbing stance, did not show a different pattern to the other two kinds of threat recorded here. Bipedal bobs, head-bobs and eyelid flashes all showed a similar pattern of decline with distance, with a higher frequency at close proximity. In addition, bipedal bobs were no more common than eyelid flashes in very close proximity, whereas one would expect their frequency increase, if males are solely indicating their willingness and preparedness to fight. Indeed, the only significant difference found was between eyelid flashes and headbobs. As such, these findings suggest other factors come into play when males engage each other in close proximity, and although the results are fully consistent with Számadó's (2008) predictions, it is also apparent that there is more to the story than proximity risk alone.

Also as predicted, I found that males were significantly more likely to threaten opponents from an A-A orientation, than from an A-P or A-S orientation, and that they were much more likely to do when in very close proximity than they were when further apart. Again, this is consistent with Számadó's (2008) ideas concerning proximity risk: males should indicate willingness and readiness to fight and, given that an A-A orientation is strongly associated with active aggression, the adoption of such a posture while producing threats would present a reliable signal of impending aggression, and willingness to back it up. At the same time, and as discussed previously, males who are genuinely attempting to engage each other in an aggressive interaction would reach a kind of 'stalemate' through jockeying for position (Pellis, 1997), giving rise to a situation in which it appeared that males were simply threatening each other, but were, in fact, attempting to strike a blow. It is also the case, of course, that if threats are to be perceived by a potential opponent then they have to be produced where the opponent can see them, and this would also account for an A-A orientation being the most common. This latter point brings in Griffiths & Scarantino's (2005) arguments regarding the very nature of a 'threat behaviour'. That is, if a threat is only a threat if the other animal responds in a particular way, then by definition, the majority of threats should occur face-to-face as this increases the probability that they will be seen clearly by the opponent and responded to accordingly. None of these explanations are mutually exclusive, however, and perhaps suggests that attempts to understand the nature of male non-vocal communication and combat should move away from trying to identify a single underlying explanation for the pattern shown. Instead, it may be more productive to recognize that all of the above are likely to play a role, and so consider ways in which the relative influence of these factors could be teased out more effectively.

The fact that all three kinds of threats showed the same pattern of decline with distance further suggests that the production of different kinds of threat behaviour cannot simply be explained by differences in levels of male arousal. That is, if threat behaviours represented a hierarchy of intensity, with eyelid threats as the lowest, and bipedal threats as highest, on the basis of their resemblance to actual fighting postures, and presumably male willingness to fight, this would provide a proximate reason for why threat displays should vary in relation to distance. The closer a male is to a potential opponent, the greater the chance of successful retaliation by the male, the higher the arousal of the approaching male, and hence the more likely he will be to produce a threat display that reflects high arousal. As all threat displays showed the same pattern, however, an explanation that considers only proximity as the explanation for male arousal will not suffice. Instead, it suggests that other factors must play a role. As discussed in the previous chapter, these could be contextual factors that were not picked up by my method of data collection, or they may be factors relating to individual identity, and to the opponent's response to an approach. This in turn suggests that a certain degree of unpredictability is a key feature of male vervet interactions, and this was borne out by the information analyses and long-range correlations.

Both of these analyses indicated that, after the initial engagement occurs between males, the nature of the ensuing interaction has a great deal of unpredictability, and shows none of the characteristics expected from a ritualized display. If one compares the transmission strength shown by male grasshoppers, for instance, the amount of information transferred in actor-reactor sequences is in the region of 40% (Steinberg & Conant, 1974), which is considerably higher than the 5% observed in my study. This in turn suggests that Griffiths & Scarantino's (2005) ideas concerning 'emotions in the wild', building as it does on Hinde's (1985) earlier work has some currency, and that certain behaviours may reflect the 'strategic' use of emotions by males, and that they are not simply expressive. More specifically, it suggests that, following a directed approach of one male to another – which represented the strongest signal for an initiator – a male may be able to predict that a potentially tense situation is about to arise, but no more. A male's response may then be geared to behaving in such a way as to acquire more information about the other (and equally the same is likely to be true of the opponent), rather than producing a particular kind of signal selected to trigger a particular kind of response. In other words, it seems possible that, as Gibson (1979) suggested, perception is a highly active process of making information available to an organism, and that the postures and behaviours produced are geared toward acquiring further information. It is notable, for example, that behaviours like head-bobs and adopting a bipedal stance are used in a variety of other contexts where the situation is ambiguous and more information would be useful. For example, animals frequently adopt a bipedal posture on hearing certain kinds of alarm calls, or when they hear screams from other troop members. They also seem to engage in head-bobbing under circumstances where visibility tends to be poor (such as in dense bush). It may be that, while such behaviours function as threats, they do not represent 'threat displays' as we usually understand them (i.e., as signals specifically selected to convey information about another individual's motivation or RHP), but are simply the most effective behaviours to use in contexts where gathering more information is crucial, such that they become strongly associated with aggression for male-male dyads. In other words, they can used *as* signals (that is, predictors) of likely aggression, but they are not themselves signals *of* aggressive intent. This interpretation fits well with the pattern of results seen, where head-bobs and bipedal stances were weak signals in terms of reducing uncertainty about what would happen next, which is what one would predict if such "signals" are, in fact, a means by which males can make more information available to themselves, and adjust their behaviour accordingly. We shouldn't, in other words, expect behaviours like these to have strong signal strength, because they represent males 'putting out feelers' to assess the other male, and not necessarily prompt him to make a particular kind of response.

This, then, gives an extra twist to Hinde's (1985) and Griffiths & Scarantino's (2005) ideas regarding emotional displays, in that 'strategically' produced emotional responses, that reflect male uncertainty, need not always be for the purpose of prompting an active response in another, but are actions "for the self", so to speak. An individual may be able to acquire further information from the other simply by taking a closer look, or looking from a different angle, both of which behaviours like head-bobbing and bipedal bobbing afford. This could provide further information on factors like, say, muscle tonus, that could act as cues to the other's emotional state, and likely responses (i.e., they could allow males to acquire information that the other animal gives off inadvertently), and also more overt signals like tail position, or genital state (adducted testicles; erect penis). If this seeking of information can explain some of the behaviours produced in a sequence, then a low transmission strength would be expected: what a male does following one of these 'information gathering' behaviours by an opponent need bear no relation at all to the nature of the information gathering or, to put it another way, one male's behaviour may effectively be independent of the other's during a portion of a sequence. As described in the methods, statistical independence of behaviours leads to transmission strengths close to zero.

It would be interesting to test this idea more thoroughly by attempting to differentiate between behaviours that could be classed as 'information gathering' rather than information transmitting, and to see how these relate to behaviours that are more clearly geared to producing a response in the other. Eyelid flashing, for example, which emerged as a strong signal seems much more obviously aimed at producing some kind of response in the other, as evidenced by the ease with which a human observer can induce a response in a vervet by performing the behaviour (and it is well known that the vast majority take direct eye-contact, a corollary of eyelid flashing as a 'direct threat': Struhsaker (1967b). From these results, then, we can formulate the further hypothesis that bipedal stances and head-bobs are information- gathering behaviours, and that eyelid flashing is a response-inducing behaviour.

The other point to be made here is that the lack of predictability in male-male interactions is perhaps a means by which we can more precisely quantify what we mean by behavioural flexibility or plasticity (Logue, Mishra, McCaffrey, Ball & Cade, 2009; Sih, Bell & Johnson, 2004). These are terms that are frequently bandied about when discussing primate behaviour but are rarely defined precisely or operationally. The approach used here, however, was able to quantify the lack of ritualization in behavioural sequences, via calculation of long-range correlation and transmission strength (which corroborated each other), and suggests a promising means by which the 'protean' nature of primate interaction can be measured.

Of course, this requires some confidence in the assessment that the behavioural sequences analysed capture the situation in a way that maps on accurately to real-life. In this analysis, for example, sit postures were lumped together for ease of analysis, but if sit-haunch does have a signal value that is different from a sit-haunch posture, either in degree or kind, then the lack of predictability in the sequence may result from the lack of resolution in the data, and not from any genuine unpredictability in the nature of male-male engagement. Similarly, higher intensity of threats were considered irrespective of lower threats (bipedal with eyelid flash= bipedal) and threats were considered irrespective of the posture in which they occurred (eyelid flash while standing= eyelid flash), again for ease of calculation, and it may be that they have different functions or signal values when this is taken into account which, again, may lead to the calculation of higher transmission strengths if they were more finely differentiated. This is clearly something that would be very interesting to consider further, and conduct more detailed analysis to ensure the lack of predictability stems from the animals and not the analyses.

It seems reasonable, however, to hypothesize that there will be genuinely high levels of unpredictability in male-male interactions, and the task before us is to understand exactly how this is brought about, and why.

CHAPTER FIVE

CONCLUSIONS AND FUTURE DIRECTIONS

5.1 Overview of the Present Study

In this thesis, I have shown that, during high aggression interactions, vervet males at Samara preferentially target the head/ neck/ shoulder area as indicated both by wound counts, and behavioural responses. This finding differs from previously reported wound data from other study sites, which suggest that both male and females received= most wounding on the haunch and tail. The finding that males at Samara show a different pattern to males elsewhere, and to females at Samara, suggests a difference in the fighting strategies of males; this in turn will most likely be linked to increased social group size, and hence more intense male-male competition, at Samara, compared to other study sites. Vervet groups at other sites are, on average, much smaller (average= 25) than the ones studied at Samara (average= 60) and differ in sex ratio (average general= 0.67; Samara= 0.55 increasing during breeding season to 0.71). Previous data across various primate species (Cords, 2000) has shown that variation in the number of males correlates with differences in social structure, such as levels of male-male affiliative behaviour and aggression, both within and between species. Ordinal rank of males in an interaction was found to predict the type and duration of postures adopted, in a manner that suggested that males were perhaps moving in relation to each other in ways designed to protect their more vulnerable genitalia, and that the head/shoulder/neck was a secondary target. Rank distance, habitat type, and number of individuals in the vicinity of male-male agonistic interactions did not predict whether interactions would escalate into physical aggression.

As predicted by Számadó (2008), proximity was found to influence the likelihood of threat behaviours, although it was not found to explain the variation in the type of threat displays and context in which they occurred. Threat displays appear not to occur in a ritualized fashion, but rather to unfold in an unpredictable manner. Information analysis and long term correlations revealed that, after the first step in an interaction, there was no predictability in what males would do in response to each other.

5.2 Implications of the Present Study

Számadó (2008) predicted that proximity would have an effect on threat displays as this is the mechanism by which the honesty of the threat can be maintained. My findings supported this, but proximity did not explain variation of different types of threats. There was some indication that eye-threats functioned in a communicative fashion: they had the strongest signal strength with respect to what the other individual would do, and were clearly directed at other indivduals. In contrast, behaviours like bipedal bobbing and head-bobbing seemed to be 'information-gathering' or 'prospecting' behaviours produced by males to assess an opponent more fully, or trigger a response in an opponent that would indicate something about the opponent's likely state or manner of response. This fits well with the idea that certain emotional behavioural responses may be strategic (Griffiths & Scarantino, 2005; Hinde, 1985). Further research is needed to test these ideas more fully. It is possible, for example, that the relatively crude resolution of the scoring used here missed certain features to which males are responsive, and more fine grained scoring could lead to more predictabilty in males' interactions. Equally it is possible that males are also able to pick up on the inadvertant cues that males produce with respect to aspects like muscle tonus, startle responses and the like, and so the monkeys themselves may have been picking up on more predictability than the analyses here allowed. More detailed analysis will help identify whether certain behaviours are more adequately described as 'prospecting' rather than threats, and also to determine whether male interactions are truly unpredictable.

If it can be shown that a lack of predictability in male interactions is genuine, then it may be that Miller's (1997) ideas regarding primate 'proteanism' have some currency in explaining the patterns shown. Miller (1997) argues that proteanism occurs as a counter-measure to predictable complex cognitive behaviour. That is, animals behave in a genuinely unpredictable manner in the sense that they have not been selected to behave predictably, even to themselves. By allowing for genuine unpredictability, there is no opportunity for individuals to signal their intentions to others, either overtly or covertly, because the individuals themselves would be unaware of any specific intention. Such a strategy could indeed be useful in situations of high competition, such as interactions between male vervet monkeys during the mating season. It could pay males to ensure their responses are unpredictable, for example, as a means for higher-ranking males to ensure that lower-ranking males are kept permanently on edge, and under higher stress levels, as these may affect their ability to obtain successful matings. This could be achieved both by ensuring that low ranking males must remain continually wary around other males whose response they cannot predict, and also because stress may affect male physiology adversely by increasing levels of corticosteroids (Sapolsky, Romero & Munck, 2000) or, as Henzi (1982, 1985) has suggested, by increasing the frequency of abduction of the testes into the body cavity, which potentially could have an adverse effect on semen quality, and influence mating success in that way. Miller (1997) further speculates that long term, cooperative interactions between individuals will lessen the occurrence of unpredictability. It may therefore be valuable to compare the interactions of females with those of males, as the greater long-term familiarity should produce lower levels of 'proteanism' in their interactions according to his hypothesis.

It is also possible, however, that males interactions are only unpredictable during times of social upheaval, like the early stages of the mating season, when new males (influx males) arrive and disrupt the male hierarchy. Such males are also an unknown quantity for resident males, and what appears to be 'deliberate' unpredictability may simply be a lack of familiarity. Linked to the above discussion of group size as a mediator of the quality of male interactions, it is also true that males at Samara will interact with a higher proportion of unknown males than is typical for a vervet troop, and this could easily change the ways in which males would conduct themselves when interacting with other males. It is possible, then, that a lack of ritualization in threat displays found at Samara may be due to this effect. More systematic sampling of male dyads, both familiar and unfamiliar over the course of the mating season would help to address this issue: one would predict lower levels of unpredictability among familiar males and a decrease in unpredictability over the course of the mating season for initially unfamiliar males (familiar males could here act as a baseline against which to compare unfamiliar male dyads).

Miller (1997) attributes the current lack of concrete evidence for social proteanism to the difficulty of recording such behaviour unless one is actively attempting to record such unpredictability (i..e, most studies focus on the central tendency in behaviour rather than variation per se). In this respect, the use of a technique like Eshkol-Wachman movement notation, as employed here, may be particularly useful as it provides an objective tool to measure patterns of movements in a way that lends itself well to information analysis.

5.3. Future directions:

5.3.1. Testing unpredictability

As noted above it is possible that male-male interactions are not entirely unpredictable, but follow a pattern that has not been picked up by the current study due to a lack of resolution in the data. In future, it would be beneficial to conduct a more detailed analysis considering more fine grained analyses of factors, such as eye gaze, scrotum abduction, penile extensions (Henzi, 1982), and also refining categorization of posture and environmental contexts.

5.3.2. Effects of group composition

Investigating the effect of male cohort size across different groups, as well as over the course of the mating season, within the same group may establish a clearer understanding of the role male cohort size plays in determining the nature of male-male interaction.

5.3.3. Ritualization of displays

Having established a general understanding of spontaneous interactions that contain high aggression and threats, I have established a foundation to compare these unpredictable events with assumed ritualized interactions, such as the "red-white-and blue" and "broadside" displays. The proximate mechanisms behind these displays have not yet been examined in detail. Conducting a more detailed analysis of these behaviours in the same fashion used here to study spontaneous agonism has the potential to offer a clearer understanding of whether such behaviours are indeed ritualized or represent a combat-driven 'stalemate' or, if they are indeed ritualized, then the origins of their communicative function can be explored with respect to spontaneous agonistic interactions, and whether ritualized displays have been co-opted from these.

5.3.4. Triadic Interactions

Finally, it would be relevant to consider triadic and polyadic interactions. In particular, extending these findings to triadic interactions presents an opportunity to focus on the dynamics of coalition formation, whereby two males join forces to defeat another. During coalitions, males are faced with the dilemma of regulating two diametrically opposed kinds of affect in partners versus opponents (simultaneously displaying coordination signals to one male while directing threatening cues to another). This also provides an opportunity to ask questions concerning audience effects during interactions and the maintenance of proximity to relevant social actors (e.g. coalition partners, fertile females). One proposal is that males predict the trajectories of other animals so they can intersect with them, such that coordination requires cooperation between individuals. Alternatively, males may use simplified rules such that coordination and cooperation is an emergent property of individual decision-making (e.g. similar to patterns seen in fish shoals). Finally, males may be entirely opportunistic with respect to their coalition partners, and so need not track them through space. Such data could also be tested against current theoretical models dealing with signalling honesty in relation to proximity, and how this might be expected to differ in triadic interactions.

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APPENDIX

1. R Code for Calculation of Long-Range Correlations

(Courtesy of Dr David Lusseau, University of Aberdeen)

```
v<-read.table("vervetseq.txt",header=T)
shannon<-function(v)
{
rep<-length(unique(v$beh))
sample<-max(v$sequence)
count<-as.data.frame(table(v$sequence))
nd<-array(0,dim=c(rep,rep,max(count$Freq)))
for (i in 1:sample) {
s<-subset(v,sequence==i)
for (j in 1:(count$Freq[i]-1)) {
for (k in j+1:count$Freq[i]) {
nd[s$beh[j],s$beh[k],k-j]= nd[s$beh[j],s$beh[k],k-j]+1
}
}
}
pd<-array(0,dim=c(rep,rep,max(count$Freq)-1))
pp<-array(0,dim=c(rep,max(count$Freq)-1))
pm<-array(0,dim=c(max(count$Freq)-1,rep))
for (i in 1:max(count$Freq)-1) {
pd[,,i]<-nd[,,i]/sum(rowSums(nd[,,i]))
pp[,i]<-rowSums(pd[,,i])
```

```
pm[i,]<-colSums(pd[,,i])
}
I<-array(0,dim=c(1,max(count$Freq)-1))


for (i in 1:(max(count$Freq)-1)) {
lp<-log(pd[,,i]/(pp[,i]*pm[i,]),base=2)
lp<-pd[,,i]*lp
lp[lp=="NaN"]<-0
lp[lp=="-Inf"]<-0
lp[lp=="Inf"]<-0
I[i]<-(sum(sum(lp)))
}
I
}
Iobs<-shannon(v)
######randomisation#####
rep<-length(unique(v$beh))
sample<-max(v$sequence)
count<-as.data.frame(table(v$sequence))
Irand<-array(0,dim=c(1000,max(count$Freq)-1))
vrand<-v
for (i in 1:1000) {
for (j in 1:sample) {
vrand[vrand$sequence==j,]$beh[2:(count$Freq[j]-1)]<-
sample(vrand[vrand$sequence==j,]$beh[2:(count$Freq[j]-
1)],size=length(vrand[vrand$sequence==j,]$beh[2:(count$Freq[j]-1)]),replace=FALSE)
#keeping approach as the first event
```

```
}
Irand[i,]<-shannon(vrand)
}


##############################
colMeans(Irand)
IrandCI<-apply(Irand, 2, quantile, probs = c(0.025, 0.975))
#######KL divergence#####
v$step<-0
for (i in 1:sample) {
v[v$sequence==i,]$step<-seq(1,count$Freq[i])
}
receiver<-table(subset(v,step==2)$beh)/sum(table(subset(v,step==2)$beh))
sender<-table(subset(v,step==3)$beh)/sum(table(subset(v,step==3)$beh))
seqrec<-seq(4,max(v$step),2)
seqsen<-seq(5,max(v$step)-1,2)
KLsend<-array(0,dim=c(1,(max(v$step)-1-5)/2))
KLrec<-array(0,dim=c(1,(max(v$step)-4)/2))
r<-1
s<-1
for (i in seqrec) {
kl<-
receiver*log(receiver/(table(subset(v,step==i)$beh)/sum(table(subset(v,step==i)$beh))),b
ase=2)
kl[kl=="NaN"]<-0
kl[kl=="-Inf"]<-0
kl[kl=="Inf"]<-0
```

```
KLrec[r]<-sum(kl)

r<-r+1





}

for (i in seqsen) {

kl<-
sender*log(sender/(table(subset(v,step==i)$beh)/sum(table(subset(v,step==i)$beh))),base
=2)

kl[kl=="NaN"]<-0

kl[kl=="-Inf"]<-0

kl[kl=="Inf"]<-0

KLsend[s]<-sum(kl)

s<-s+1

}

plot(1:length(KLsend),KLsend)

plot(1:length(KLrec),KLrec)

###and then separate by rank difference
```

APPENDIX

2. Complete sequence of behaviours used in the information and entropy analyses

#	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	A	SIT	E	STD	BP	STD	E	STD	SIT	BP	BP	STD																	
2	A	STD	E	STDX	STD																								
3	A	STD	E	STD	HB	STD	STD	E	STD	SIT																			
4	A	STD	E	STD	HB	STD	E	STD	E	STD	E	STD	HB	STD	SIT	E	SIT	E	SIT	E	SIT	STD							
5	A	SIT	STD	E	STD	SIT																							
6	A	STD	STD	E	STD	SIT																							
7	A	STD	STD	E	STD	HB	SIT	STD																					
8	A	STD	E	SIT	E	SIT	E	SIT	HB	SIT	E	SIT	STD																
9	A	STD	STD	E	STD	BP	STD	STD																					
10	A	SIT	STD	HB	STD	STD																							
11	A	STD	E	SIT	STD																								
12	A	STD	E	STD	E	STD	E	STD	STD																				
13	A	STD	STD	E	SIT	STD																							
14	A	STD	STD	HB	STD	E	STD	STD																					
15	A	STD	STD	HB	STD	HB	STD	E	STD	SIT	E	SIT	STD																
16	A	STD	E	STD	BP	STD	E	STD	E	STD	STD																		
17	A	SIT	STD	E	STD	STD																							
18	A	SIT	STD	E	STD	E	STD	E	STD	E	SIT	HB	STD	HB	SIT	E	SIT	E	SIT	STD									
19	A	SIT	STD	E	SIT	HB	SIT	E	SIT	HB	SIT	STD																	
20	A	STD	STD	E	SIT	STD																							
21	A	STD	E	STD	HB	STD	E	SIT	E	SIT	HB	SIT	E	SIT	SIT														
22	A	SIT	STD	E	STD	SIT																							
23	A	SIT	STD	E	STD	STD																							
24	A	STD	E	SIT	STD																								

25	A	STD	BP	SIT	E	SIT	STD	HB	STD	HB	STD	BP	STD	BP	STD	HB	STD	STD											
26	A	STD	HB	STD	E	STD	HB	STD	STD																				
27	A	STD	E	SIT	E	SIT	STD																						
28	A	STD	STD	E	SIT	STD																							
29	A	STD	STD	E	STD	STD																							
30	A	SIT	STD	E	STD	SIT																							
31	A	SIT	STD	E	SIT	HB	STD	SIT	E	SIT	STD	HB	STD	BP	STD	E	STD	E	SIT	HB	SIT	STD							
32	A	STD	E	STD	STD																								
33	A	SIT	STD	E	STD	SIT																							
34	A	SIT	STD	HB	STD	E	STD	STD																					
35	A	SIT	STD	HB	STD	E	STD	E	SIT	STD																			
36	A	STD	BP	STD	STD																								
37	A	STD	E	STD	E	STD	E	STD	E	STD	HB	STD	SIT																
38	A	STD	E	BP																									
39	A	STD	STD	BP	STD	HB	STD	STD																					
40	A	SIT	STD	E	STD	STD																							
41	A	STD	STD	E	STD	E	STD	E	STD	STD																			
42	A	SIT	STD	HB	STD	HB	STD	STD																					
43	A	SIT	STD	BP	STD	STD																							
44	A	SIT	E	SIT	SIT																								
45	A	SIT	E	SIT	STD																								
46	A	STD	E	STD	BP	BP	E	STD	STD																				
47	A	STD	E	STD	STD	BP	STD	STD	HB	STD	BP	STD	STD																
48	A	SIT	STD	BP	STD	E	STD	BP	STD	E	STD	BP	STD	BP	STD	BP	STD	BP	STD	E	STD	E	STD	BP	STD	E	STD	STD	
49	A	STD	E	STD	BP	STD	E	STD	BP	STD	E	STD	STD																
50	A	SIT	STD	HB	SIT	E	SIT	STD																					
51	A	SIT	SIT	E	SIT	SIT																							
52	A	SIT	SIT	E	SIT	SIT																							
53	A	SIT	BP	SIT	BP	SIT	E	STD	E	SIT	STD																		
54	A	SIT	HB	SIT	STD																								

55	A	SIT	STD	BP	STD	BP	STD	STD																					
56	A	BP	STD	E	STD	BP	STD	BP	STD	E	STD	E	STD	BP	STD	E	STD	E	STD	BP	STD	E	E	STD	BP	SIT	E	SIT	STD
57	A	STD	STD	E	STD	HB	SIT	STD																					
58	A	SIT	E	SIT	E	SIT	E	SIT	BP	SIT	STD																		
59	A	STD	E	STD	STD																								
60	A	SIT	E	SIT	STD																								
61	A	STD	STD	BP	STD	STD																							
62	A	SIT	E	SIT	HB	STD	HB	STD	HB	SIT	HB	SIT	E	STD	HB	SIT	HB	SIT	SIT										
63	A	STD	E	STD	E	STD	E	STD	E	STD	HB	STD	E	STD	E	STD	STD												
64	A	SIT	E	SIT	SIT																								
65	A	STD	BP	STD	BP	STD	STD																						
66	A	STD	E	STD	BP	STD	E	STD	STD																				
67	A	STD	STD	BP	STD	E	STD																						
68	A	STD	BP	HB	STD	BP	SIT	STD	HB	STD	STD																		
69	A	STD	E	STD	SIT																								
70	A	STD	E	SIT	STD																								
71	A	STD	E	SIT	STD																								
72	A	STD	E	STD	E	STD																							
73	A	SIT	E	STD	E	STD	STD																						
74	A	STD	BP	STD	E	STD	STD																						
75	A	SIT	E	SIT	STD																								
76	A	STD	E	STD	E	SIT	STD																						
77	A	STD	BP	STD	E	E	STD	E	STD	BP	STD	E	E	STD	E	STD	STD												
78	A	SIT	E	SIT	STD																								
79	A	STD	BP	STD	STD																								
80	A	SIT	STD	HB	SIT	BP	STD	SIT																					
81	A	BP	E	STD	BP	STD	STD																						
82	A	SIT	STD	BP	BP	STD	HB	BP	BP	STD	HB	STD	BP	SIT															
83	A	SIT	STD	HB	STD	STD																							
84	A	STD	E	STD	BP	STD	E	STD	HB	STD	HB	SIT	BP	SIT	STD														

85	A	SIT	E	SIT	STD	BP	STD	E	STD	BP	STD	HB	STD	HB	STD	BP	STD	BP	STD	STD									
86	A	STD	E	STD	STD																								
87	A	STD	BP	STD	HB	E	SIT	STD																					